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CONTRIBUTIONS TO THE KNOWLEDGE OF THE FLORA OF THE GREY LIMESTONES OF VENETO: PART II

A REVISION OF THE *FLORA FOSSILIS FORMATIONIS OOLITHICAE* OF DE ZIGNO

(With 3 Plates and 10 Text-figures)

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PREFACE

My studies of DE ZIGNO's rich collection of fossil plants from the « grey limestones » (*calcari grigi*) of Veneto, Northern Italy, are continued in this present Memoir which includes new descriptions and illustrations of some of the plants that were described and figured by DE ZIGNO in the second volume of his *Flora fossilis formationis oolithicae* (1873-85).

The specimens which DE ZIGNO ascribed to the form-genus *Podozamites* have been transferred to other form-genera since it is considered that there was inadequate evidence for assigning them to BRAUN's genus, even in its broadest sense.

The pinnate fronds that DE ZIGNO described as belonging to the genus *Sphenozamites* BRONGN. have been re-examined and the validity of the form-genus has been established, though within stricter limits than it was formerly understood. An investigation of the cuticles of these specimens has revealed that the genus is yet another representative of the Bennettitales. As a result of these new investigations it has been necessary to institute a new form-genus (*Apoldia* gen. nov.) to include some other fronds which were originally called *Sphenozamites*, but which differ from the Italian species in the structure of their cuticle.

Once again I wish to offer my sincerest thanks to Professor Giambattista DAL PIAZ, Director of the Institute of Geology of the University of Padua, for his very great kindness in allowing me continued access to the collection of specimens at Padua, and for facilitating the publication of my Memoirs on the fossil plants. In addition, I must thank many British friends for their continued encouragement, especially Miss L. I. SCOTT for her valuable and critical advice, and Mr. G. W. RIPLEY for again so ably preparing the photographic plates.

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June, 1958.

DESCRIPTION OF THE FOSSIL REMAINS

In my first paper on the fossil plants from the « grey limestones », the conifers were, for the sake of convenience, divided into forms with thick, spirally arranged leaves the venation of which is not known (Form-genera *Brachyphyllum* BRONGN., *Pagiophyllum* HEER, and *Dactylethrophyllum* WESLEY), forms with 1-veined leaves (Form-genus *Elatocladus* HALLE *sensu lato*) and forms with several-veined leaves (Form-genus *Podozamites* BRAUN *sensu lato*). The first four genera were described and it was my intention that the forms with several-veined leaves should be described and illustrated in the present paper [WESLEY, 83].

Descriptions of these forms now follow, but I am not convinced that the name *Podozamites* should be used for them. In the second volume of the *Flora fossilis....* [88], DE ZIGNO described and figured certain specimens which he assigned to this genus (*Podozamites zeillerianus* ZIG., *P. plicatus* HEER, *P. hacketi* FEISTM., and *P. rigidus* ZIG.). He was not absolutely certain of his determinations, but he considered *Podozamites* to be the most suitable genus to which the specimens could be allocated.

All the specimens, which were named *Podozamites*, are isolated, elongated leaf-like structures with parallel venation (indeed, some of the smaller specimens appear to have possessed only one vein), and there is no evidence whatsoever as to whether they represent detached pinnae of a compound leaf or whether they are, in actual fact, entire leaves in themselves.

I have come to the conclusion, therefore, that the data are inadequate for retaining the name *Podozamites* for these specimens, and I have decided to transfer them to the form-genera *Desmiophyllum* LESQ. (forms with several veins) and *Pityophyllum* NATH. (forms with a single vein). This means that *Podozamites* is not represented in the Italian flora, and that the number of undoubted coniferous genera stands at four — *Brachyphyllum*, *Pagiophyllum*, *Dactylethrophyllum* and *Elatocladus* — or perhaps five if *Pityophyllum* is also included.

Pityophyllum is generally considered to have been a conifer, but there is no corroborative evidence for this from the Italian specimens. The systematic position of *Desmiophyllum* is also rather uncertain, though investigations by other workers suggest that it includes plants of gymnospermous affinities.

On the evidence available, I believe that it is only possible to class the Italian specimens, which I am now re-naming *Desmiophyllum* and *Pityophyllum*, as plants of uncertain position - probably gymnosperms.

GYMNOSPERMAE INCERTAE SEDIS

Form-genus DESMIOPHYLLUM LESQUEREUX.

1878. *Desmiophyllum* - LESQUEREUX [45], p. 322.
1904. *Desmiophyllum* LESQ. emend. - SOLMS-LAUBACH [77], p. 6.
1919. *Desmiophyllum* LESQ. - SEWARD [75], p. 70.
1928. *Desmiophyllum* LESQ. - SAHNI [62], p. 8.
1935. *Desmiophyllum* LESQ. - HARRIS [30], p. 98.
1950. *Desmiophyllum* LESQ. - LUNDBLAD [49], p. 49.
1955. *Desmiophyllum* LESQ. - KRAUSEL [41], p. 17.

Discussion of Genus: The form-genus *Desmiophyllum* is nowadays employed as a convenient name for isolated linear leaves of Mesozoic age which have parallel veins and, in the absence of evidence as to the shoots which bore them, cannot be assigned to more precisely defined genera. The name was originally established by LESQUEREUX [45] for some narrow sub-linear leaves from the Coal Measures of Pennsylvania, and in his sense it probably represents a synonym for *Cordaites*. The present use of the name dates back to SOLMS-LAUBACH [77].

There are several genera which are brought to mind when looking at detached ribbon-shaped laminae with parallel veins and, unless further data are available about the mode of attachment or the structure of the cuticle, the choice of name to be applied is not easy. Unless other and more complete specimens are known it is impossible to decide whether the detached structures represent entire leaves in themselves or individual segments of a compound leaf. This is particularly the case with the genera *Podozamites* BRAUN and *Phoenicopsis* HEER.

Podozamites, originally intended for pinnate leaves of the cycadalean type [BRAUN, 4], was extended by SCHENK [64] to include an axis bearing a number of simple parallel-veined leaves, with small scale leaves at the lower end. This is the sense in which the name is now understood, and there is little doubt that some of the species, perhaps the greater number, are coniferous [HARRIS, 30; SEWARD, 75], but it is equally likely that others (comprising true pinnate leaves) are cycadophytes.

Phoenicopsis was instituted by HEER [36] for linear leaves attached in clusters to dwarf shoots covered basally with small scale leaves, and more recent studies of the cuticles of several species point to ginkgoalean affinities [HARRIS, 30].

Often isolated leaves of these two genera may be fairly safely named when they are in close association with more or less complete specimens of which a specific identification may be made, but in many cases there is no evidence whatsoever as to their mode of attachment. For such examples the non-committal name *Desmiophyllum* is preferable. Unfortunately it has not often been the custom to use this name and there have been many records of the occurrence of *Podozamites* and *Phoenicopsis* which are not supported by adequate data as to mode of attachment. Many of these uncertain identifications have been made because the distinctive characters which the original authors of the genera had in view have not been followed.

The position is also made more complicated by the existence of other genera such as *Feildenia* HEER [HEER, 37; SEWARD, 75; HARRIS, 30] (syn: *Torellia* HEER [HEER, 35; HARRIS, 30]), *Nageiopsis* FONTAINE [FONTAINE, 20; SEWARD, 75], *Bambusium* UNGER [UNGER, 80], *Yuccites* SCHIMPER & MOUGEOT [SCHIMPER & MOUGEOT, 67], *Pelourdea* SEW. [SEWARD, 74] and possibly others, but in some cases evidence from cuticular structure has provided further criteria by which specimens may be identified.

The structure of the cuticle of at least two species of *Desmiophyllum* is known - *D. indicum* SAHNI [62] and *D. cyclostomum* LUNDBLAD [49]. The former « belongs to a type so widely distributed among gymnosperms that it can hardly serve as a guide to general affinities » [SAHNI, 62; p. 10], while the Swedish species has a type suggesting « possible Cycadalean affinities » [LUNDBLAD, 49; p. 50]. In addition, it should be noted that SEWARD has described the anatomical structure of *D. solmsi* SEW. and shown that it probably is of ginkgoalean type [SEWARD, 75].

DESMIOPHYLLUM ZEILLERIANUM (ZIG.) n. comb.

Plate I, figs. 1-3. - Text-fig. 1 A-D.

1885. *Podozamites Zeillerianus* - DE ZIGNO [88], p. 130; Tab. XLI, figs. 1-6.

Type-specimen: Not defined by DE ZIGNO.

Syntypes: DE ZIGNO [88]; Tab. XLI, figs. 1, 5 & 6 (De Zigno Collection No. 4665), fig. 2 (No. 4666), fig. 3 (No. 4667), fig. 4 (No. 4668).

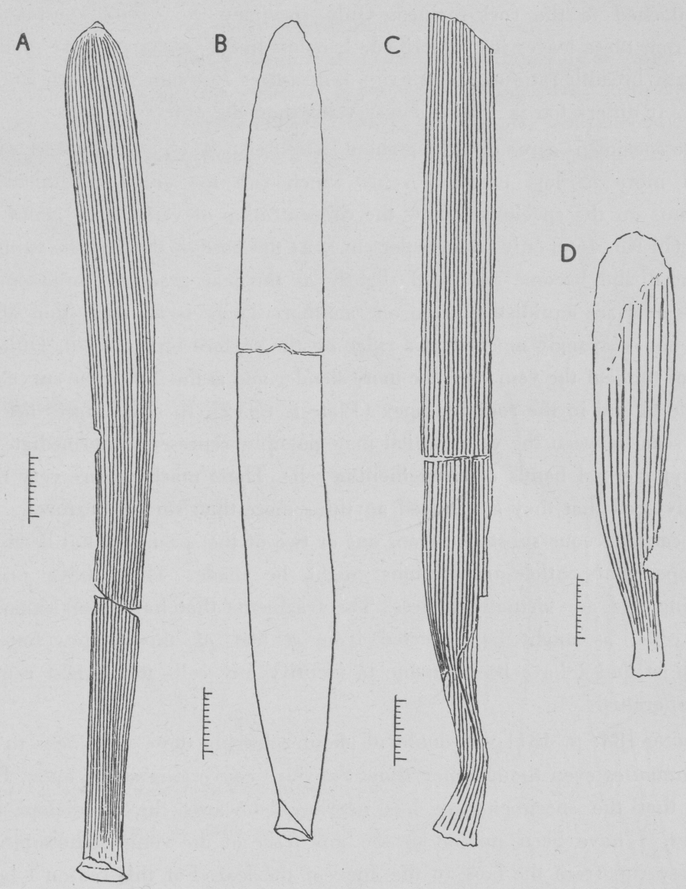
Locality: Valle Zulliani, near Roverè di Velo.

Diagnosis: Leaf linear, strap-shaped or spathulate, from five to more than twelve times long as broad; narrowing gradually towards base and then widening again slightly at insertion; leaf-base elliptical in section; apex obtuse, rounded; margins entire. Veins 10-15, simple, unbranched, equal, strongly marked, equidistant, more or less parallel, all running entire length of lamina, abruptly convergent near apex and becoming slender where they curve in.

Description and Discussion: Only seven specimens, all of which were collected from the dark grey limestone in the Valle Zulliani, near Roverè di Velo (Province of Verona), can be identified with certainty as belonging to this species. All were named *Podozamites zeillerianus* by DE ZIGNO in his catalogue, and those specimens not figured in the second volume of the *Flora fossilis*.... are Nos. 4662, 4663 (the counterpart of No. 4667) and 4664.

It is not known if the specimens represent detached leaflets of a compound leaf or whether they are complete leaves in themselves. An examination of the several specimens in DE ZIGNO's collection leads me to interpret them as complete leaves. None of the pinnate fronds in the collection has pinnae approaching the dimensions of these specimens, nor do any of them possess leaflets with the same type of venation. Certainly none of the pinnate fronds show any indications of elliptical scars on the rachis, such as would be left by the present specimens had they been pinnae.

All the specimens, with one exception (No. 4668), consist of linear, strap-shaped leaves with parallel or nearly parallel margins. Towards the basal end there is a very gradual narrowing but, just before attachment, the margins again diverge. Here the leaf is elliptical in cross-section which suggests that scars of a similar shape would have been left on the axis that originally bore them. Distally the margins, which are entire throughout, suddenly converge to an obtuse, rounded, apex. One specimen (No. 4665, Text-fig. 1 A; Plate I, figs. 1, 2) shows another feature in the form of a small apical



TEXT-FIG. 1. *Desmiophyllum zeillerianum* (ZIG.) n. comb.

A. Specimen No. 4665, shown also in Plate I, fig. 1, drawn to show the correct number of veins; figured by DE ZIGNO as a syntype of *Podozamites zeillerianus* ZIG. [88; Tab. XLI, fig. 1]. Scale equals 10.0 mm.

B. Specimen No. 4666; venation not shown; figured by DE ZIGNO as a syntype of *Podozamites zeillerianus* ZIG. [88; Tab. XLI, fig. 2]. Scale equals 10.0 mm.

C. Specimen No. 4667, shown also in Plate I, fig. 3, drawn to show the correct number of veins; figured by DE ZIGNO as a syntype of *Podozamites zeillerianus* ZIG. [88; Tab. XLI, fig. 3]. Scale equals 10.0 mm.

D. Specimen No. 4668 showing the correct number of veins; figured by DE ZIGNO as a syntype of *Podozamites zeillerianus* ZIG. [88; Tab. XLI, fig. 4]. Scale equals 10.0 mm.

hump. It is not known whether this is an artifact of preservation or whether it may have been an apical prolongation. At least, it is quite clear that the veins did not run into it.

In general, the leaf is approximately ten to twelve times long as it is broad, as measured on complete specimens - No. 4665 is 148.0 mm. long and 11.5 mm. at its widest point, and No. 4666 is 141.0 mm. long and 14.0 mm. wide. The ratio of length to breadth must have been higher for specimen No. 4667 (and its counterpart No. 4663) for it is incomplete and measures 143.0 mm. in length and 12.5 mm. in breadth, yet there is no indication of the terminal region on that part of the specimen which still remains attached to the rock-surface. Only specimen No. 4668 exhibits a greater variation from these leaves just described. It is less linear in shape, more spathulate and with a length/breadth ratio of about five - it measures 76.0 mm. in length and 14.0 mm. in breadth. It differs too in having fewer veins than the others.

All the specimens agree in having about fifteen (No. 4668 has only ten) unbranched, equal and more or less parallel, veins which run the entire length of the leaf. Measurements on the specimens show the concentration of veins to be about 13-14 per cm. width (in No. 4668 only about 9 per cm.). At the base of the leaf the veins are more closely spaced and become separated slightly as the leaf gradually broadens out, but everywhere they are equidistant from one another. There is no suggestion of a midrib and each vein is strongly marked as a ridge on the surface of the fossil. Quite near the distal end of the leaf the veins become more slender and at the same time curve in towards the mid-line to end in the rounded apex (Plate I, fig. 2). In some places fine striations have been seen between the veins which may possibly represent intermediate veins or, perhaps, hypodermal bands of strengthening cells. These markings are very faint and I am not convinced that they are indeed anything more than surface features.

Some carbonaceous substance from one or two of the specimens has been macerated in the hope that cuticle-preparations might be made. These have proved very disappointing and are virtually useless. The fragments that have been examined show elongated cells, as might be expected from a leaf of this shape, but they are very indistinct and I have been unable to identify any cells that might represent the stomatal apparatus.

De Zigno [88; p. 131] was doubtful about referring these specimens to the form-genus *Podozamites* even though they show the veins converging at the apex. He pointed out, also, that the specimens are less narrowed towards the base than in a true *Podozamites*. I have been unable to see any trace of the veins dichotomising at any point as they run from the base to the apex of the leaf. For this reason I believe that they cannot be allocated to *Podozamites* since in that genus the veins always divide near the base of the lamina.

Luigia Grandori [22] included the name « *Phoenicopsis latifolia* n. sp. » in her list of gymnosperms, and I believe that this name refers to the present specimens. There is no evidence that justifies their inclusion in the genus *Phoenicopsis* as there is no suggestion that they were borne in clusters on a relatively short axis covered with small scale leaves, nor do the veins dichotomise near the base.

I propose, therefore, to transfer the specimens to the non-committal genus *Desmiophyllum*.

DESMIOPHYLLUM RIGIDUM (Zig.) n. comb.

Plate I, fig. 4. - Text-fig. 2 A-C.

1885. *Podozamites rigidus* - De Zigno [88], p. 134; Tab. XLI, figs. 10, 10 a, 10 b.
1885. *Podozamites plicatus* Heer - De Zigno [88], p. 131 (ex parte); Tab. XLI, fig. 7.

Type-specimen: Not defined by De Zigno.

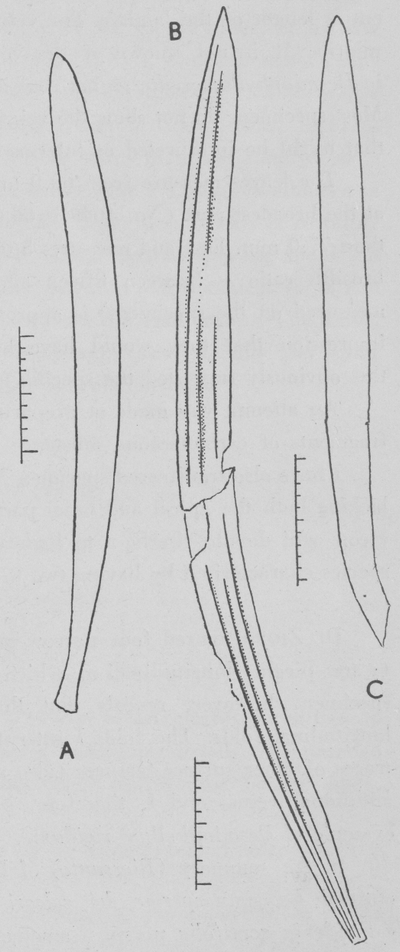
Syntypes: De Zigno [88]; Tab. XLI, fig. 10 (De Zigno Collection No. 4648), fig. 10 a (No. 4644), fig. 10 b (No. 4649).

Localities: Valle Zulliani, near Roverè di Velo; Pernigotti.

Diagnosis: Leaf rigid, linear, from fifteen to eighteen times long as broad; narrowing gradually towards base and then widening again slightly at insertion; abruptly narrowing distally to an acute apex; margins entire. Veins 3 - 5, simple, unbranched, equal, not strongly marked, equidistant, more or less parallel, running entire length of lamina.

Text-fig. 2.

Desmiophyllum rigidum (Zig.) n .comb.



A. Specimen No. 4649 shown also in Plate I, fig. 4; figured by De Zigno as a syntype of *Podozamites rigidus* Zig. [88; Tab. XLI, fig. 10 b]. Scale equals 10.0 mm.

B. Specimen No. 4648; figured by De Zigno as a syntype of *Podozamites rigidus* Zig. [88; Tab. XLI, fig. 10]. Scale equals 10.0 mm.

C. Specimen No. 4646; the basal part is lacking. Scale equals 10.0 mm.

Description and Discussion: *Desmiophyllum rigidum* is represented by seven specimens in De Zigno's collection at Padua. In addition to those listed above, the following specimens are typical: Nos. 4646, 4647, and 4650 (all collected in the Valle Zulliani and catalogued as *Podozamites rigidus* Zig.).

De Zigno [88; p. 134] was uncertain to which genus these specimens should be referred, but for the sake of convenience he chose *Podozamites*. As with *Desmiophyllum zeillerianum* it is not known whether the specimens represent detached pinnae of a compound leaf or whether they are entire leaves. On the available evidence I prefer to regard them as individual leaves and accordingly suggest the use of the non-committal form-genus *Desmiophyllum*.

The leaves are fairly slender, gradually narrowing towards the base, but quite near the base the margins again diverge so that the leaf must have had a fairly broad insertion. Specimen No. 4648 (Text-fig. 2 B) is broken at the basal end and this broadening out is not shown. Towards the distal end, the entire margins converge to an acute apex.

Each leaf has three to five, more or less parallel, longitudinal veins which run the entire length of the lamina. The veins are all equal and equidistant, and there is no midrib. It is not known if the veins converge at the apex or end separately as in *Desmiophyllum zeillerianum*, but it is quite certain that they all run into the apex. Most specimens do not show the veins very clearly, and there are no obvious striations that might be interpreted as intermediate veins.

The leaves measure from 60.0 to 80.0 mm. in length and from 3.0 to 5.0 mm. wide at the broadest part (No. 4649 is 66.0 mm. long and 4.0 mm. wide; No. 4648 is more than 77.0 mm. long and measures 5.0 mm. at its maximum width), so that the length/breadth ratio is between fifteen and eighteen, and the concentration of veins (as measured on the specimens) is approximately 3 per 0.5 cm. width. The leaves give an impression that they would have been quite rigid in the living condition, and this obviously suggested the specific name to De Zigno.

An attempt was made at preparing the cuticle from some of the specimens, but the fragments of carbonaceous substance completely disintegrated during maceration.

I have also transferred specimen No. 4660 to this species. It is a very poor specimen lacking both the apical and basal parts [88; Tab. XLI, fig. 7]. De Zigno referred it « con ogni dovuto riserbo » to *Podozamites plicatus* Heer [De Zigno, 88; p. 132], a species characterised by having two to four longitudinal folds and about thirty simple veins.

De Zigno figured four narrow grooves and recorded the three longitudinal folds (« tre pieghe longitudinali ») which they separate, but a close examination of the specimen, however, reveals that there are really five narrow grooves and four longitudinal folds. The folds I interpret as corresponding to veins, for I can find no traces of other surface-features (also not recorded by De Zigno) that might represent additional veins, and I, therefore, prefer to regard the specimen as an incomplete example of *Desmiophyllum rigidum*.

In the summary (*Riassunto*) of her *Dissertazione di laurea in Scienze Naturali*, entitled *Le gimnosperme dei calcari grigi e la loro età geologica*, Grandori lists « *Feildenia acutifolia* n. sp. » amongst the gymnosperms of the « grey limestones »,

and in a preliminary note to her studies published in 1913 [22] there appears the name « *Phoenicopsis acutifolia* n. sp. ». There are no descriptions of these species and it is not known to which specimens they may have referred. However, I believe that she was using these two names for the present specimens, for in her list there are no other names which could possibly refer to them. There is no cognate evidence from the specimens to justify the use of either of these names and, therefore, I suggest *Desmiophyllum* as preferable.

Form-genus PITYOPHYLLUM Nathorst.

1897. *Pityophyllum* - Nathorst [55], p. 62.
1919. *Pityophyllum* Nath. - Seward [75], p. 380.
1933. *Pityophyllum* Nath. - Yabe *and* Oishi [84], p. 230.

Discussion of Genus: The form-genus *Pityophyllum* was applied by Nathorst [55] to detached leaves of needle-like form similar to those of the recent pines, or to long linear leaves, broader and flatter than those of *Pinus*. It is a comprehensive genus including also leaves very similar to those of the living genus *Keteleeria*. Seward writes « *Pityophyllum*, if employed for both the narrower and broader forms, includes specimens which in all probability belong to Conifers of more than one family: some are certainly Abietineous but the flatter and broader forms bear a closer resemblance to leaves of some species of *Podocarpus*, *Cephalotaxus* or *Torreya* ». There is certainly much variation in the length/breadth ratios of many of the figured species, and I am sure that many of the specimens named *Pityophyllum* have no real botanical value and probably represent leaves of plants that belonged to several different groups. The name, however, serves a very useful purpose, so long as its application to any particular specimen does not carry any implication as to its precise relationships.

PITYOPHYLLUM CRASSICOSTATUM sp. nov.

Plate I, fig. 5. - Text-fig. 3 A-C.

1885. *Podozamites Hacketi* Feistm. - De Zigno [88], p. 132 (ex parte); Tab. XLI, figs. 8-9.

Type-specimen: De Zigno Collection No. 4659.

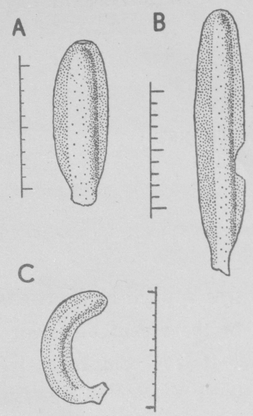
Locality: Pernigotti.

Diagnosis: Leaf linear, from three to five times long as broad; narrowing at base to a short stalk about one third width of lamina; abruptly narrowing distally to a rounded apex; margins entire. Leaf with a broad median ridge ending just behind apex. (Venation not known).

The specific name *crassicostatum* is suggested by the broad median ridge which is so characteristic of all the specimens.

Description and Discussion: There are five specimens in the collection at Padua that show these very well-defined characters and which must, therefore, be regarded as

representing a single species. These are, in addition to No. 4659 which is catalogued as « *Podozamites Hacketi* FEISTM. » and described as such by DE ZIGNO [88; p. 133], specimens Nos. 4651, 4652 and 4653 (all catalogued as « *Podozamites parvulus* SAP.? ») and 4639. All are preserved in the buff-coloured limestone of Pernigotti.



TEXT-FIG. 3.

Pityophyllum crassicostatum sp. nov.

A. Specimen No. 4652; Scale equals 10.0 mm.

B. Type-specimen No. 4659 shown also in Plate I, fig. 5; figured by DE ZIGNO as *Podozamites hacketi* FEISTM. [88; Tab. XLI, fig. 8]. Scale equals 10.0 mm.

C. Specimen No. 4639. Scale equals 10.0 mm.

The largest specimen, No. 4659, measures 22.5 mm. in length and has a maximum width of 4.5 mm. It has a short stalk about 3.0 mm. long and 2.75 mm. wide, and it is quite symmetrical in shape. It has a rounded apex and the broad median rib, which stops short just behind the apex, is very marked. The other specimens are somewhat smaller, and of slightly different relative dimensions. In all cases the very marked broad rib, the rounded apex and the short stalk are very characteristic. Specimen No. 4639 (Text-fig. 3 C) is interesting for it may represent a leaf distorted in growth. It still, however, shows the very prominent rib which here, as in the other specimens, is seen to be continued into the short stalk by which the leaves were attached to the axis that bore them. Some similar curved leaves of *Podozamites lanceolatus* (L. & H.) SCHIMP. were figured by YABE and OISHI [84; Pl. 34, figs. 12-13].

DE ZIGNO [88; p. 133] referred these specimens « con qualche esitanza » to *Podozamites hacketi* FEISTM. [FEISTMANTEL, 13]. He chose this species for it was the only one known to him in which the individual leaf-segments had a very marked median rib. He regarded the Italian specimens as representing young examples since the Indian forms had pinnae twice as large. I cannot agree with DE ZIGNO's determination of these specimens, for there is no indication whatsoever as to how they were borne on the parent plant. There are no data as regards the venation, though the thick rib suggests that there may have been only one median vein. For this reason it seems to me that the form-genus *Desmiophyllum* is unsuitable, and that the name *Pityophyllum* is preferable.

YABE and OISHI [84] figured some leaves of *Pityophyllum krasseri* YABE & OISHI which are somewhat similar to those from Pernigotti. They differ, however, in being sessile and in having acutely pointed apices.

Unfortunately none of the Italian specimens have plant-substance preserved from which cuticle-preparations might have been made.

CYCADOPHYTA

By far the greater part of the second volume of the *Flora fossilis....* is devoted to descriptions and illustrations of species which DE ZIGNO regarded as representatives of the « Cycadeaceae ». Most of the specimens are of fronds, some of which are extremely fine examples, but there are a few reproductive structures. Apart from types occurring in Jurassic floras in other parts of the world, DE ZIGNO described a total of thirty-five species from the Venetian Alps distributed amongst ten genera as follows:

Fronds	Reproductive Structures
Pterophyllum BRONGN. (2 species)	*Androstrobus* SCHIMP. (1 species)
Zamites BRONGN. (4 species)	*Cycadospadix* SCHIMP. (1 species)
Ptilophyllum MORRIS (1 species)	*Cycadeospermum* SAP. (5 species)
Otozamites BRAUN (12 species)	*Blastolepis* ZIG. (3 species)
Sphenozamites BRONGN. (4 species)	
Podozamites BRAUN (2 species excluding *P. plicatus* and *P. hacketi*)	

Certain of DE ZIGNO's species were not accepted by later workers, who either reduced the number of them or identified them with other forms. Unfortunately many of these changes were made without detailed examinations of DE ZIGNO's own collection of specimens at Padua. While some of these changes may very well have served a useful purpose at the time when they were made, a number of them have now become invalidated as a result of my investigations of the cuticles of certain of the species, and I suspect that this may also eventually be the case with many of the other changes.

When DE ZIGNO wrote his *Flora fossilis....* the only members of the Cycadophyta then known were the living cycads, and it was natural that he and other contemporary workers should group the Mesozoic cycad-like fronds with the Cycadales. Some years were to elapse before it was demonstrated that, during the Mesozoic period, the Cycadophyta were also represented by another order which no longer has any living members. This extinct order, known as the Bennettitales, includes plants which bore fronds fairly closely resembling, in their gross morphology, those of many cycadalean species.

In addition to the different construction of their reproductive organs, the Bennettitales also differ markedly from the Cycadales in the very distinctive structure of their stomatal apparatus which is of the syndetocheilic type (see p. 15 *et seq.* for details). Thus it has come about that, following the results of detailed investigations of their cuticles, many species, which were formerly considered to have represented fossil cycads, have now been shown to have belonged to the Bennettitales.

DE ZIGNO's collection contains many fine examples which still have plant-substance preserved on the rock-surface, and I am certain that when I have completed my

investigations of their cuticles it will be necessary to transfer the majority of species to the Bennettitales.

Already my investigations of several of the species have revealed interesting results which are being presented in this present paper. Only one genus, *Sphenozamites* Brongn., is being dealt with here - observations on some of the other genera will appear in the next paper and it is hoped to eventually publish an account of the reproductive structures.

BENNETTITALES

Form-genus SPHENOZAMITES Brongniart emend.

1833. *Odontopteris* Brongn. - Sternberg [78, Teile 5-6], p. 78 (ex parte).
1836. *Odontopteris* Brongn. - Goeppert [21], p. 208 (ex parte).
1838. *Zamites* Brongn. - Presl. in Sternberg [78, Teile 7-8], p. 197 (ex parte).
1843. *Zamites* Brongn. - Morris [54], p. 25 (ex parte).
1849. *Sphenozamites* - Brongniart [5], p. 61 (ex parte).
1849. *Cyclozamia* - Pomel [58], p. 345 (ex parte).
1849. *Sphenozamia* - Pomel [58], p. 345 (ex parte).
1850. *Zamites* Brongn. - Unger [81], p. 282 (ex parte).
1851. *Sphenozamites* Brongn. - Miquel [51], p. 210.
1861. *Sphenozamites* Brongn. - Miquel [52], p. 31.
1869. *Otopteris* L. & H. emend. - Schimper [65], p. 484 (ex parte).
1870-72. *Sphenozamites* Brongn. - Schimper [66], p. 162.
1875. *Sphenozamites* Brongn. - Saporta [63], p. 181.
1881. *Sphenozamites* Brongn. - De Zigno [88, livr. 2-3], p. 105.
1900. *Sphenozamites* Brongn. - Zeiller [85], p. 232.
1904. *Sphenozamites* Brongn. - Seward [72], p. 117.
1917. *Sphenozamites* Brongn. - Seward [74], p. 587.
1932. *Sphenozamites* Brongn. emend. - Linell [48], p. 242.

Some of the citations in this list refer only to names, but in all cases they include plants that have been assigned to the genus *Sphenozamites* at some time or other. The most important discussions of the genus are those of Schimper [66], Saporta [63], De Zigno [88], Seward [72; 74] and Linell [48].

Emended Diagnosis: Frond openly pinnate, narrowing towards base and apex, without a terminal pinna; rachis thick, terete or sub-terete, longitudinally striated; pinnae alternate, remote, asymmetric, orbicular to lanceolate-falcate, most commonly obliquely rhomboid, inserted obliquely on sides of rachis and never covering it; bases of pinnae narrowing in a wedge-shaped manner to a sessile insertion, never auricled; apices of pinnae obtuse or acute, margins entire, sinuate or spinulose-dentate. Veins numerous, slender, dichotomous, radiating towards margins and apices; outermost acroscopic veins parallel with basal acroscopic edges of the pinnae. Cuticle of rachis thick: epidermal cells squarish; stomata rare, sunken: stomatal apparatus syndetocheilic with two lateral subsidiary cells. Upper cuticle of pinna without indication of veins: epidermal cells isodiametric, polygonal or four-sided; anticlinal walls distorted into loop-

like folds: stomata absent. Lower cuticle of pinna with rather well-defined stomatal bands (lying between veins) and non-stomatal bands (lying over veins), except near edge of lamina where stomata absent; stomatal bands not sunken, consisting of fairly well-defined rows of stomata separated by ordinary epidermal cells; stomatal rows not sunken: epidermal cells rectangular or irregularly four-sided, usually arranged in rows; anticlinal walls distorted into loop-like folds; some cells represent trichome-bases: stomata mostly orientated transversely; guard cells sunken in shallow pit formed by the two lateral subsidiary cells; subsidiary cells with or without papillae; guard cells cutinised in upper and outer walls.

Discussion of Genus: The name *Sphenozamites* was proposed in 1849 by Brongniart [5] as a sub-genus of cycadalean fronds that had previously been assigned to the form-genus *Otozamites* Braun [4]. The new name was to be used for pinnate fronds on which the pinnae, with their characteristic diverging dichotomous veins, were narrowed to a wedge-shaped base and not auricled as in the genus *Otozamites* proper. He quoted « *Cyclopteris Beani* L. & H. » [46] as illustrative of the new sub-genus, and added *Pterophyllum oblongifolium* Kurr [42] and *Zamites undulatus* (Sternb.) Presl (78, Teile 7-8) as other examples. He suggested that the name might eventually be raised to generic rank and this was done, though in too wide a sense, by De Zigno in the second volume of his *Flora fossilis*.... [88].

The generic identity of *Sphenozamites* has been recognised by Schimper [66], Saporta [63], Renault [60], Zeiller [85], Seward [72; 74] and Linell [48] who have found it a convenient name for describing forms not easily allocated to other genera, but it should be noted that some of these authors have used the name in a more restricted sense than others.

The position and natural affinities of *Sphenozamites* remained unknown until Linell [48] re-examined the Keuper species *Sphenozamites tener* Compter [6; 7], though in general it had been the custom to regard the genus as including fronds of plants belonging to the Cycadophyta (i. e. of cycadalean or bennettitalean affinity) rather than to the Pteridophyta. Linell's investigations of the cuticle of *S. tener* (which only seemed to have been noticed by Potonié [59] and Mägdefrau [50]), proved the cycadophyte affinities of the fronds of that species, and the general characteristics of the epidermis and structure of the stomatal apparatus led to his assigning the species to a position near the Nilssoniales.

Nothing was known about the other species of *Sphenozamites*, but my recent investigations of the structure of the cuticle of the Italian specimens, assigned by De Zigno [87; 88] to this genus and accepted as valid species of *Sphenozamites* on morphological grounds by Linell [48], have enabled me to demonstrate beyond doubt that these are true representatives of the Bennettitales.

The chief characteristics of the cuticles of the two Italian species, *Sphenozamites rossii* Zig. and *S. geylerianus* Zig., of which full descriptions and illustrations follow (p. 27 *et seq.*), conform exactly with those features which distinguish the leaves of the Bennettitales from those of other pinnate-leaved fossil gymnosperms. The cuticle of the Bennettitales is characterised by the very distinctive structure of the stomatal apparatus and the thickenings of the guard cells. The stomatal apparatus is of the syndetocheilic

type, which, apart from the living genera *Welwitschia* and *Gnetum*, is only found in the extinct Bennettitales [Florin, 16; 17; 18; Harris, 28]. This type of stomatal apparatus consists of two guard cells bordered laterally by two subsidiary cells, all four cells having been formed by parallel divisions of a single initial cell. In addition, the dorsal and outer walls of the guard cells (upper and outer walls respectively of my terminology - see p. 36) are distinctively cutinised, and often the cutinisation of the dorsal (upper) wall is particularly strongly developed in the region where it extends into the common wall between the guard cell and the adjacent lateral subsidiary cell. Less constant characters of the group are the transverse orientation of the stomata and the arrangement of the epidermal cells in well-marked rows and usually with very sinuous anticlinal walls [Harris, 28].

Thus *Sphenozamites* as formerly defined now no longer represents a natural grouping of species and it is obvious that the name cannot be validly applied to all the previously described forms. It becomes immediately necessary to re-define the form-genus in *sensu stricto* to cover one assemblage of species only. What characters, therefore, can be used to distinguish those species possessing the bennettitalean type of stomatal apparatus (a) from forms with a similar gross morphology but possessing a non-bennettitalean type of stomatal apparatus and (b) from closely allied forms belonging to the Bennettitales?

In the first place it will be convenient to consider the species of which the cuticular structure is now known. These are *Sphenozamites tener* Compter [Linell, 48; Mägdefrau, 50], *S. rossii* Zig. (p. 27 *et seq.*) and *S. geylerianus* Zig. (p. 42 *et seq.*).

Sphenozamites tener was shown by Linell to have a cuticle-structure which he regarded as being very close to that of the Nilssoniales. The epidermal cells of this species are of irregular shape, somewhat isodiametric, and arranged in an irregular manner and not in well-defined rows. The cell walls are thin and straight and most cells show a papilla on the outer surface. Unicellular hairs are recorded. Non-stomatal bands over the veins alternate with stomatal bands between the veins; both are seven to eight cells wide. Within the stomatal bands the stomata are densely crowded but there is little indication of their being arranged in regular rows. Towards the margin of the pinna the stomata become scarcer and the epidermal cells larger, with thicker walls. This part Linell interprets as the « bordure cartilagineuse » of Saporta [63]. On the upper surface the epidermal cells are arranged mainly in longitudinal series and are of an hexagonal shape, with walls thicker than those of corresponding cells on the lower surface. Stomata are normally absent from the upper surface except for a narrow region a short distance in from the margin. Compter [6] also recorded the absence of stomata from the upper surface, but both he and Linell had only fragmentary material to deal with.

The stomata of *Sphenozamites tener* have a variable appearance due to the irregular arrangement of the epidermal cells. Typically the stomatal apparatus shows the pore between two sunken guard cells which are scarcely visible since they are surrounded by, and in part roofed over by, a crown of dark-coloured neighbouring cells, which are strongly thickened towards the aperture of the stomatal chamber and which possess a strong cuticular papilla. Linell reports that it appears that the stomatal apparatus is constructed in such a manner that, after the original stoma-mother-cell had divided

longitudinally to form the two guard cells, these became sunken below the general level of the epidermis so that an outer chamber was formed. Adjacent epidermal cells, without undergoing a division, have widened towards this outer chamber and consequently partly over-roofed the guard cells. At the same time the walls of these cells have become strongly cutinised where they surround the opening of the stomatal chamber. No division of these crown or neighbouring cells, as Linell has called them, has taken place, so that they have directly become subsidiary cells without division of the original mother-cell. The neighbouring cells vary in number from four to eight, but six seems to be the most general. A similar feature was reported by Compter [6] in his original investigations of the cuticle. Linell considers that the neighbouring cells are for the most part already distinct from the stoma-mother-cells in the meristem — that is to say that the stomatal apparatus is of the haplocheilic type — and with him I must agree. The number of neighbouring cells reaches its maximum when the stoma-mother-cells lie in a meristem giving rise to irregularly arranged cells, but when they lie in a meristem giving rise to regular rows of cells the number of neighbouring cells is smaller. This explanation of Linell for the variation in number of neighbouring cells in each stomatal apparatus is probably based upon an assumption that there may be more cells in contact with a stoma-mother-cell in a meristem that gives rise to irregularly arranged cells than in a meristem that does not. One of his illustrations (Taf. VI, fig. 5) shows two of the neighbouring cells looking like ordinary epidermal cells, and in another (Taf. VI, fig. 7) there are apparently only two neighbouring cells lying opposite to one another on either side of the chamber; the three remaining cells of this particular crown are weakly coloured and with only an insignificant development towards the chamber. Linell remarks that this arrangement is superficially reminiscent of that in the Bennettitales where there are two lateral subsidiary cells outside the guard cells. From his observations on the stomatal apparatus of *Sphenozamites tener* it is quite certain that this similarity is only apparent and not real, for I am convinced that he has shown quite conclusively that the stomatal apparatus is of the haplocheilic type and that it could in no manner be mistaken for the syndetocheilic type which characterises the Bennettitales. Linell considers that the single ring, or crown, of neighbouring cells is very reminiscent of *Nilssonia* as described by Thomas & Bancroft [79] and Florin [15], and that *Sphenozamites* is not a member of the Bennettitales.

As has already been stated above, and as will be shown in full in later pages of this work, the two Italian species (*Sphenozamites rossii* and *S. geylerianus*) have typical bennettitalean cuticles. It is necessary now to seek characters by which these two species may be distinguished from *Sphenozamites tener*.

Linell used De Zigno's diagnosis [88] in his assessment of the previously described forms that had been assigned to *Sphenozamites*, and then he presented a re-definition of the genus as follows:

« Blätter locker paarfiederig mit Endfieder; Fiedern gegenständig oder alternierend, etwas einwärts an der Oberseite einer kräftigen Rachis inseriert, mehr oder weniger gespreizt, der Form nach mehr oder weniger asymmetrisch, wobei der hintere Rand länger als der vordere ist; Basis der Fiedern sich keilförmig verschmälernd oder sich scharf zu einem Stiel verjungend nie einem ansehnlicheren Teil der Rachis bedeckend,

nie geöhrt. Nerven von der Basis der Fiedern aus gegen den Rand zu divergierend, mehrfach gegabelt, in den äusseren Teilen sehr dichtangeordnet..... ».

This emended diagnosis of LINELL includes characters which are exhibited by *Sphenozamites tener* as well as other species also assigned to the genus. The morphological part of the definition (reproduced above) can, therefore, be interpreted within broad limits.

The two Italian species agree only with respect to certain characters, but differ in other aspects. *Sphenozamites rossii* and *S. geylerianus* agree as follows: the leaf is loosely constructed; the pinnae are alternate and more or less spreading, and of more or less asymmetric form; the bases of the pinnae narrow in a wedge-shaped manner, never cover an appreciable part of the rachis, and are never auricled; the fan-like dichotomous venation. They do not show the following features which are those most typical of *Sphenozamites tener* itself: leaf with paired pinnae and a terminal pinna; pinnae opposite and inserted somewhat towards the upper side of the rachis; posterior margin of pinna longer than anterior; base of pinna sharply narrowed to a short stalk.

It is logical, therefore, that these two sets of characters should form the main morphological criteria by which the Italian species may be separated from *Sphenozamites tener*. This separation will thus involve the institution of a new form-genus in addition to *Sphenozamites* proper, since the name can no longer be applied to fronds with such widely differing cuticular structure.

Sphenozamites rossii was described and illustrated by DE ZIGNO [87] in 1868, while COMPTER [6] first used the name *Sphenozamites tener* in 1883. By applying the rule of priority the generic designation must, therefore, be retained for the Italian species and all other similar fronds that may eventually be proved to have the bennettitalean type of cuticle. The name *Sphenozamites tener* thus no longer remains a valid combination and I propose to rename the species *Apoldia tenera* (COMPTER) n. comb. and designate it the generitype of the form-genus *Apoldia* gen. nov., which I define as follows:

Frond openly pinnate, with paired pinnae and a terminal pinna; rachis thick; pinnae opposite, remote, more or less asymmetric with posterior margin longer than anterior, inserted somewhat towards the upper side of rachis and never covering an appreciable part of it; bases of pinnae narrowing in a wedge-shaped manner and then sharply narrowed to a short stalk, never auricled. Veins numerous, dichotomously forked many times, diverging from base of pinna to margins. Epidermis (so far as known) consisting of cells arranged in irregular rows; ordinary epidermal cells irregularly four-sided or polygonal, with straight (non-undulating) walls; stomata present mainly on lower surface between veins; stomatal apparatus haplocheilic with two sunken guard cells and a crown of neighbouring cells (equivalent to subsidiary cells); neighbouring cells varying in number and more or less strongly cuticularised.

The name of the new form-genus *Apoldia* is suggested from Apolda, the type-locality.

While the bennettitalean nature of the Italian species has been clearly demonstrated, it is still not possible to state any particular features of the cuticle-structure that could be used in defining *Sphenozamites* as a natural genus. Such a problem always confronts one in descriptions of the different leaf-forms that belong to the Bennettitales, and we

are still forced to fall back upon the use of form-genera with diagnostic features based on external morphology alone. This problem is admirably discussed by HARRIS, who points out that there is so often an intergrading between closely similar leaf-genera, which are all, therefore, somewhat artificial, and that their boundary must be arbitrary and should be so regarded [34].

HARRIS accepts the three leaf-genera *Ptilophyllum*, *Zamites* and *Otozamites* as defined by HALLE [23] on the shape of the bases of the pinnae, and he expresses these characters in tabular form as follows:

	Superior basal angle	Inferior basal angle
Ptilophyllum	contracted	decurrent
Zamites	contracted	contracted (symmetrically)
Otozamites	expanded and then contracted (i. e. an auricle present)	contracted (asymmetrically)

adding to the list *Pterophyllum*, in which neither basal angle is contracted, and *Anomozamites*, which is like *Pterophyllum* but has short pinnae [34].

Another relatively constant character of these form-genera that might usefully be added to this list is that of position of attachment of the pinnae on the rachis. In *Ptilophyllum*, *Zamites* and *Otozamites* the pinnae are inserted on, or very much towards, the adaxial (upper) face of the rachis, whereas in *Pterophyllum* and *Anomozamites* the leaf-segments are inserted more or less laterally on the rachis and never cover its adaxial surface [ARNOLD, 2].

The question of the retention of *Sphenozamites* as a valid form-genus of bennettitalean fronds now remains to be discussed. I believe that *Sphenozamites*, which I propose should be defined within stricter limits (p. 14) than previously, cannot be suitably combined with any of the five form-genera named above. The lateral insertion of the pinnae immediately separates the fronds from those assigned to *Ptilophyllum*, *Zamites* and *Otozamites*, all of which have the pinnae inserted distinctly upon the upper face of the rachis. This only leaves the genera *Pterophyllum* and *Anomozamites* available. However, these last two named form-genera are characterised by having fronds with pinnae which do not have either basal angle contracted. This is not the case with *Sphenozamites* where each of the pinnae narrows gradually towards the base in a wedge-shaped manner.

It will be convenient, at this point, to compare the previous definitions of the form-genus *Sphenozamites* as used by earlier investigators. SCHIMPER [66] defined the genus as follows:

« *Folia rachi valida subtereti stricta instructa. Foliola remota, transverse articulato-inserta, majuscula, late obovata, basi plus minus angustata, subpedicellata, aequilateralia, subintegra vel apice dentata, nervis e basi radiantibus, numerosis, dichotomis* ».

SAPORTA [63] used the following diagnosis, which was quoted by SEWARD [72]:

« *Frondes plerumque rachi valida tereti instructae pinnatae, pinnae vel foliola latiores majusculae basi plus minusve angustata subpedicellatae aequilaterales cartilagineo-cinctae integrae aut apice sinuatae dentataeque spinosae, racheos lateribus ordine alterno insertae nec unquam basibus inter se connexis racheos superficiem tegentes, nervulis e loco insertionis radiantibus numerosis dichotome pluries divisis* ».

DE ZIGNO [88] emended the diagnosis of *Sphenozamites* and his definition was used by LINELL [48] in his assessment of the forms which had previously been assigned to the genus. DE ZIGNO defined the characters as follows:

« *Folia laxe pinnata, rachide valida subtereti instructa. Pinnae majusculae, alternae, remotae, ovatae vel oblongae, aut oblique rhomboidales, integerrimae, vel marginibus repando sinuatis, aut spinuloso-dentatis, apice obtusae vel acuminatae, base cuneiformi vel rotundata plus minusve angustata, subpedicellatae, lateribus rachidis adfixae, nec rachidem unquam tegentes. Nervi tenues, creberrimi, pluries dichotomi a puncto insertionis flabellatim radiantes* ».

These are the definitions which have been used by later authors as the basis of their identifications of fronds which they considered were representatives of the genus. In some cases, these identifications have been insecurely founded and it is quite obvious that a number of species should, more correctly, be placed in other genera. These doubtful identifications have usually been founded on rather broad interpretations of the generic limits of *Sphenozamites*. All the early authors agree on the loose construction of the leaf which has pinnae inserted alternately and laterally on the rachis. The narrowing of the pinnae at their bases in a wedge-shaped manner has always been regarded as the main generic feature. The absence of an auricle on the forwardly directed margin of each pinna which would overlap the rachis has always been understood, but has never been included in the generic definitions. This is the character that seems to have caused most trouble in separating *Sphenozamites* from *Otozamites*, for many of the narrow-leaved forms of *Otozamites* often do not show the auricle particularly well-developed. As far as the shape of the pinnae is concerned there is no doubt that *Sphenozamites* approaches quite closely to some of species of *Otozamites*. I do not believe, however, that the venation of the pinnae of *Sphenozamites*, as now more strictly defined in my emended diagnosis, gives any hint of an auricle on the forwardly directed margin. All the specimens that I have examined show quite clearly that the outermost acroscopic veins are parallel for a short distance with the basal part of the forwardly directed margin of a pinna, and there is no indication anywhere that their course is altered or that they end where an auricle ought to be. This I regard as a very significant difference between *Sphenozamites* and *Otozamites*.

In the case of *Otozamites beani* (L. & H.) BRONGN., it is not easy to understand why BRONGNIART should have quoted it as illustrative of *Sphenozamites* for it has pinnae which most definitely have their distal basal edges expanded into rounded auricles covering the upper surface of the rachis as in a true *Otozamites*. SCHIMPER [66] and later workers correctly pointed out that *Otozamites beani* (« *Cyclopteris Beani* » of LINDLEY & HUTTON) is a true *Otozamites* and not a representative of *Sphenozamites*, though they did accept the name *Sphenozamites* for certain species.

There remain to be discussed two points that were mentioned by the earlier authors. SCHIMPER, SAPORTA and DE ZIGNO described the pinnae as « subpedicellate » and regarded *Sphenozamites rossii* as the most typical member of the genus. However, I cannot agree that this is a character of the Italian species, and I am quite satisfied that none of DE ZIGNO's specimens have pinnae showing any indication of short stalks where they are attached to the rachis; in other words, the pinnae are sessile. The other Italian species, *S. geylerianus*, also has pinnae which lack short stalks and since both species possess the bennettitalean type of cuticle I prefer to restrict the name *Sphenozamites* to fronds on which the pinnae are not stalked.

SAPORTA writes — « Les folioles des *Sphenozamites* paraissent cernées d'une mince bordure cartilagineuse, ainsi que cela a lieu dans la plupart des Cycadées » — and included this character in his diagnosis of the genus [63]. I feel, however, that he somewhat overstressed this point. Certainly the margins of *S. rossii* appear to have been quite tough, but *S. geylerianus* gives no suggestion that its pinnae had cartilaginous borders. LINELL [48] regarded the marginal region of the pinnae of *S. tener*, where the epidermal cells became larger, longer and thicker-walled, as equivalent to the « bordure cartilagineuse », and with this I would agree, but even in that species the pinnae, though distinctly outlined on the rock-surface, do not appear to have had a particularly tough margin. Certainly pinnae with a thick upper and lower cuticle would be expected to have a « bordure cartilagineuse » at the margins, but I do not consider this to be of generic significance since it is bound to be a variable character according to the relative thicknesses of the cuticle of the two surfaces.

General Survey of Species assigned to Sphenozamites: Apart from the Italian species and *Apoldia tenera* nothing is known of the cuticular structure of any of the other forms that have previously been called *Sphenozamites*. Now that it has been shown that the name has been applied to plants belonging to two separate groups, the suspected heterogeneity of the genus is finally proved. Any assessment of the species of which the structure of the cuticle is not known must be, therefore, somewhat tentative, though it ought to be possible to indicate if the name can still validly be applied within the limits as now re-defined.

I have made an extensive search through the literature and in one case only have I been unable to refer to either an illustration or description. The list of species which follows is thought to be complete, though there is always the possibility that some may have escaped my notice. Examination of the available figures or descriptions leads me to believe that some of the determinations are definitely incorrect.

In addition to « *Cyclopteris Beani* L. & H. » [46], BRONGNIART included *Pterophyllum oblongifolium* KURR [42] and *Zamites undulatus* (STERNB.) PRESL [78, Teile 7-8] as representing his new sub-genus *Sphenozamites* [5]. « *Cyclopteris Beani* » is, of course, undoubtedly a true *Otozamites* [SCHIMPER, 66; SAPORTA, 63; DE ZIGNO, 88; SEWARD, 72; 74; HARRIS, 32], but the generic position of the other two species is less certain.

The Liassic specimen, which KURR called *Pterophyllum oblongifolium*, was an insignificant piece consisting of a rachis with four oval, symmetrical pinnae with rather broad insertions, blunt apices and diverging veins. KURR's generic naming of this

specimen can hardly be correct for the genus *Pterophyllum* is characterised by pinnae which are not contracted at their insertion on the rachis; its right position is difficult to determine however. It differs from *Sphenozamites* by the broad insertions of its pinnae, but approximates to the genus in their venation and distant spacing. SEWARD [74] says that it is probably an *Otozamites*, but this does not agree with his own definition of the genus (auricled, asymmetrical bases). The bases of the pinnae are reminiscent of those of some species of *Zamites*, but there is a marked difference in the venation. SCHIMPER [66] used the name *Glossozamites* for intermediate forms, and we might follow his example and place *Pterophyllum oblongifolium* in that genus.

Zamites undulatus, recorded from the Inferior Oolite of Yorkshire, is the only one of BRONGNIART's original species which can be more suitably named *Sphenozamites*. The species, which was originally named *Odontopteris undulata* by STERNBERG [78, Teile 5-6], has distantly placed pinnae with wedge-shaped (almost symmetric) bases and no indications of auricles. The form of the pinnae is like that of a typical *Sphenozamites* which is characterised by the asymmetry of the distal parts of its pinnae. There has, however, been some confusion in the descriptions especially with reference to the insertion of the pinnae. Both SCHIMPER [66] and DE ZIGNO [88], who accepted it as a typical *Sphenozamites*, describe it as having the pinnae inserted on the adaxial face of the rachis. On the other hand, RENAULT says distinctly that the pinnae are inserted on the sides of the rachis [60]. Obviously, therefore, the original specimens need to be re-examined. SEWARD [71; 74] regarded this species as probably identical with *Otozamites acuminatus* (L. & H.) BRONGN.; the difference, however, is very striking. LINDLEY & HUTTON's species [47] has closely spaced pinnae which are inserted on the adaxial face of the rachis, and which have broad asymmetrical bases, that have an auricle on their forwardly directed edge, and gradually become symmetrical and taper to a sharp point. It is quite definitely a typical *Otozamites*, and an examination of SEWARD's figures of *Otozamites acuminatus* (including *O. acuminatus* var. *brevifolius*) does not reveal any close resemblance to *Sphenozamites*, so that it is difficult to comprehend why he should have regarded the two forms (i. e. *Zamites undulatus* and *Otozamites acuminatus*) as examples of a single species. While the exact mode of attachment of the pinnae is still uncertain I feel that STERNBERG's species is better named *Sphenozamites undulatus*. SCHIMPER [66] was the first to publish a diagnosis of the species under its new name and it should, therefore, correctly be cited as *Sphenozamites undulatus* (STERNB.) SCHIMP.

Sphenozamites latifolius (BRONGN.) SAP. has been collected from rocks of Inferior Kimmeridgean age at Orbagnoux in France [SCHIMPER, 66; SAPORTA, 63; DE ZIGNO, 88; MORET, 53]. Though the cuticle is unknown, I favour the retention of this form as a species of *Sphenozamites*. The lateral insertion (though transverse) and the broadly ovate-orbicular pinnae, which are very similar in shape to the basal ones of *S. rossii* though lacking the characteristic margins of that species, suggest that it is correctly named. In 1895, SEWARD described a new genus *Withamia* with *W. armata* (*Cycadorachis armata* of SAPORTA [63] as the generitype [70]), and gave the description of a similar species which he called *W. saportae*. Unfortunately, the figures of this species from the Wealden of England carry the name « *Withamia armata*, gen et sp. nov. » [SEWARD,

70; Plate II, figs. 1 and 2; Plate V, fig. 1], so that it is not known whether he was using the specific epithets « *saportae* » and « *armata* » as synonyms. It would certainly appear that this was his intention, for *W. saportae* is never referred to again in any of his later writings. *W. saportae* was described as having a broad axis (? rachis) « bearing stout recurved spines arranged laterally in two rows, and at slightly irregular intervals. In the axils of the spinous processes there are attached more or less orbicular or obcuneate leaf-like structures, having a distinct flabellate (*Cyclopteris* type) venation ». Accompanying the description were long extracts of a letter from SAPORTA in which this great French authority remarked upon the resemblance of the leaf-like structures of *Cycadorachis* (*Withamia*) *armata* to the pinnae of *Sphenozamites latifolius*. ZEILLER [85] renamed the genus *Sewardia* since UNGER [81] had previously used *Withamia* for a stem of which the anatomical structure was known. ZEILLER also combined the species of *Withamia* SEW. with *Sphenozamites latifolius* as *Sewardia latifolia*, the new combination being accepted by SEWARD [74; 75]. Though we have no evidence that the species are identical, nor, for that matter, that they represent separate types, I prefer to retain *Sphenozamites latifolius* as a name for specimens without spines on the rachis. I have not seen the French specimens of *Sphenozamites latifolius*, but the published figures do not show scars where spines might originally have been attached. In *Sewardia* these spines still remain after the axillary structures have fallen, whereas in *Sphenozamites latifolius* nothing remains on the rachis after fall of the pinnae.

Some detached pinnae from the Inferior Kimmeridgean at Orbagnoux and the Cornbrash at Etrochey were called *Sphenozamites brongniartii* by SAPORTA [SAPORTA, 63; DE ZIGNO, 88]. Unfortunately it is not known how the pinnae were inserted on the rachis. The description seems to suggest that the pinnae bear some slight resemblance to those of the Wealden *Otozamites klipsteinii* (DUNK.) SEW.; I would not say more than this and until better specimens become available it would not be useful to pursue the matter further.

In addition to the previously mentioned forms, DE ZIGNO [88] included two others under *Sphenozamites* - *S. medianus* (LECK.) ZIG. and *S. phillipsi* ZIG. *Sphenozamites medianus*, from the Inferior Oolite of Yorkshire, was the leaf that LECKENBY had described and figured as *Otopteris mediana* [44]. SEWARD [71] did not agree with DE ZIGNO and regarded *S. medianus* as a synonym of *Otozamites beani*. HARRIS [32] is also of the same opinion, as indeed I am myself having examined the original illustration of LECKENBY. Certainly the pinnae as figured have wedge-shaped bases, but there is a suggestion of an auricle on the forwardly directed margin of each into which the veins run, in addition to the fact that the pinnae are inserted on the adaxial face of the rachis. This was noted in the diagnosis and description given by DE ZIGNO.

Sphenozamites phillipsi, also from the Oolite of Yorkshire, was the name given to a specimen that had previously been figured by PHILLIPS as *Cycadites latifolius* [57; Plate X, fig. 1]. DE ZIGNO did not see the actual specimen and his description is based on the published figure alone. In many ways PHILLIPS' specimen, as figured, is reminiscent of *Sphenozamites* since the pinnae appear to be inserted laterally on the rachis, and are broadly asymmetrical without any indication of auricles on their forwardly directed edges. The diverging veins, however, tend to run more parallel with the basiscopic

margins of the pinnae than with the acroscopic as in *Sphenozamites*. I have not seen the original specimen myself, but SEWARD states that it « consists of an imperfectly preserved portion of a frond which cannot be satisfactorily defined as a species distinct from *O. acuminatus*, but is, I believe, identical with this species. The drawing given by Phillips is by no means accurate; the veins in the pinnae are numerous, and not as represented in the figure » [SEWARD, 71]. On the basis of present information, therefore, the naming of this frond is uncertain. An examination of the cuticle, if any still remains, is urgently needed as well as a new description and illustration. At present it could be a *Sphenozamites*, especially if the pinnae are of the shape shown and are really inserted on the sides of the rachis.

Sphenozamites rochei is a species from the Lower Permian of Autun which was first described by RENAULT [60] in 1881. The pinnae are inserted laterally on the rachis and are of a shape very similar to those of *S. geylerianus*, but they show a marked difference from those of that species in having the cuneate bases slightly decurrent below. This feature is almost of sufficient importance for separating this Palaeozoic form from the Mesozoic species, but until such time as we have some knowledge of its cuticle it is more convenient to leave the name unaltered. Both SEWARD [74] and LINELL [48] accepted the species as a typical *Sphenozamites*.

The largest species to which the name *Sphenozamites* has been given is *Sphenozamites rogersianus* from the older Mesozoic (Rhaetic) of Virginia [FONTAINE, 19] and the Triassic of York County, Pennsylvania [WARD, 82]. FONTAINE's American species had fronds at least one metre in length with the largest pinnae measuring 190.0 x 90.0 mm., and it corresponds with the general conception of *Sphenozamites* in having its pinnae inserted laterally on the rachis or only a trifle towards the upper side of it. However, *S. rogersianus* is distinguished from typical species of *Sphenozamites* by the shape of its pinnae, each of which is narrowed at its base to an indistinct stalk and which is more symmetrical and more or less elliptical with the maximum breadth nearer to its apex than base. The pinnae are more uniform in breadth than those of *Apoldia tenera*, another species of relatively large dimensions, but the whole habit of the frond, as well as the insertion and venation of its pinnae, led LINELL to accept it as a true *Sphenozamites* [48]. SEWARD, on the other hand, pointed out what he considered to be a close resemblance between *S. rogersianus* and *Pterophyllum bronni* SCHENK, and suggested that the Virginian species should be spoken of as « *Pterophyllum* (*Macropterygium*) *rogersianum* » [74]. I am certain that SEWARD was not correct in using the name *Pterophyllum*, since that genus is characterised by pinnae which are not contracted at their insertions on the rachis, but his suggestion that SCHIMPER's genus *Macropterygium*, which has the pinnae contracted at their insertions [66], might be used seem to me to be a much more suitable suggestion. In *S. rogersianus*, FONTAINE observed between the veins « a fine granulation, which, seen under a lens, is composed of globular prominences or dots ». Later he adds « nothing definite can be seen in the granulation that covers the leaflets. This granulation does not appear to be anything like a fructification ». LINELL investigated this peculiar granulation and came to the conclusion that it was not just a simple surface-feature (SEWARD [74] had suggested that it was due to the presence of papillae), but he could not determine its true nature. FONTAINE's suggestion that it had nothing to do with reproductive structures was confirmed by a

maceration of the carbonised leaf-substance which did not reveal any spores. LINELL was of the opinion that the granulation might possibly be compared with the small carbon-filled hollows of *Taeniopteris multinervis* WEISS which HALLE [25] took for resin-glands. Certainly no such structures have been seen in either of the Italian species, but that does not necessarily mean that they may be lacking in all species of *Sphenozamites*.

A species of uncertain age (Trias - Jura) from Tasmania was described by JOHNSTON under the name of *Sphenozamites feistmantelli* [40]. The fronds of this species have elongated pinnae inserted laterally on the rachis in an alternate or sub-opposite arrangement. Up to six veins, which dichotomise a few times, run from the insertion towards the margins and apex. The pinnae are very irregular in outline and have a number of lobes of indefinite shape and size, some of which end in teeth or spines into which a vein often runs [JOHNSTON, 40; Plate XXIV, figs. 1 and 2]. I do not believe this to be a typical *Sphenozamites* and agree with SCHUSTER [68] that it ought to have another name. SCHUSTER instituted his new genus *Walkomia* (non FLORIN) for this particular species.

NEWBERRY [56] described two species from the Rhaetic of Honduras — *Sphenozamites robustus* and *Sphenozamites? grandis* — but he only gave figures of the first named. *S. robustus* must have been a large frond (its form is unknown) since the pinnae vary from one to four inches in length. They are ovoid or lanceolate in outline, thickened and narrowed at the base, and pointed at the apex. The margins are entire and there are a few veins which dichotomise as they run fanwise to all parts of the margin. NEWBERRY regarded it as a cycad and named it *Sphenozamites* since the pinnae are distinctly wedge-shaped at the base and more or less asymmetric in outline, and he considered that, if the curvature of the pinnae was towards the apex of the frond, the general aspect of the leaf would have been very like that of *S. geylerianus*, but much larger. SEWARD pointed out a resemblance to his *Sphenozamites belli* [74], but having examined NEWBERRY's figures I am more inclined to compare his species with *S. latifolius* as figured by SCHIMPER [66] and SAPORTA [63].

Only incomplete and isolated pinnae of *Sphenozamites ? grandis* are known. They were four, or more, inches in length, of oblong or lanceolate shape, obtuse and narrowed towards the base. The veins are strong, straight, simple or rarely forked, in part diverging from the base to the margins, in part running parallel to the upper margin. The true position of these pinnae is difficult to determine, but from NEWBERRY's description it seems that they might more suitably be placed in *Glossozamites* SCHIMP. [66]. According to NEWBERRY the species reminded him of particularly large forms of *Glossozamites stoliczkanus* FEIST. from the Lower Gondwanas of India [FEISTMANTEL, 14]. The pinnae of the Indian species clearly do not belong to *Sphenozamites*, and SEWARD was of the opinion that it belonged to *Cordaites* [74].

Sphenozamites multinervis KURTZ was founded on a single leaf-pinna from the Permo-carboniferous of the Argentine [KURTZ, 43]. KURTZ was in doubt as to whether the specimen should be called *Sphenozamites* or *Noeggerathiopsis* FEISTM. [FEISTMANTEL, 14]. The tongue-like form and marked symmetry of the specimen, as well as its venation, are against KURTZ's decision. All these characters suggest that the specimen should be more correctly allocated to *Noeggerathiopsis*, which occurs with typical examples in the Argentinian Gondwana flora [LINELL, 48].

Sphenozamites geinitzianus KURTZ is also quoted as occurring in the flora of the same formation in the Argentine [BODENBENDER, 3]. Neither SEWARD [74] nor LINELL [48] had seen figures of this species so that we have no corroborative evidence.

To some large, wedge-shaped, detached pinnae from the Middle Jurassic of Stonesfield, SEWARD [72] gave the name *Sphenozamites belli*. Though the structure of the cuticle of this species is unknown, I have every reason to regard it as a valid species of *Sphenozamites* for the pinnae have the distinct type of venation with the outermost acroscopic veins parallel with the forwardly directed edges such as is shown by both the Italian species.

Sphenozamites linsiana STOCKMANS & MATHIEU is the name of an isolated pinna from the permo-carboniferous strata of Kaiping [STOCKMANS & MATHIEU, 89]. The leaflet is elliptic in shape, measuring 45.0 mm. in length and 20.0 mm. broad, with a broad attachment about 6.0-7.0 mm. It is attenuated towards its apex and somewhat rounded, though an inspection of the illustration [89; Pl. VII, fig. 5] leads me to suggest that it may have been originally acute. Many strong veins run fanwise towards the entire margins and apex, though without any trace of dichotomy. Even though the leaflet is almost symmetrical in outline the venation shows some asymmetry, and it seems to me that the specimen has been conveniently named within the limits of available evidence.

From what has been written I think that it becomes obvious that much detailed and careful re-investigation of the previously described specimens is urgently required for a proper assessment of the genus. SEWARD's statement that « the genus though serving a useful descriptive purpose is founded solely on form, and in the absence of other data, it would be rash to assume that its use implies close natural affinity » [74] has now been shown to be true following the descriptions of the cuticles of *Sphenozamites tener* [LINELL, 48] (now to be known as *Apoldia tenera*) and *S. rossii* and *S. geylerianus* (p. 27 *et seq.*). This does not mean, however, that the name cannot be retained as a distinctive form-genus. Provided that its limits are strictly defined, as I have now proposed, its retention may well serve a useful purpose. It is in applying the name to specimens from several widely-separated horizons in the vertical time scale that great care should be taken. I am certain that the use of *Sphenozamites* for fronds ranging from the Permo-carboniferous to the Jurassic is not justified, but while the state of our knowledge is so meagre I feel that to multiply the number of generic names would only lead to confusion. When the cuticle is not known the name *Sphenozamites* should only be applied with the greatest caution.

For the most part other organs of the plant which bore *Sphenozamites*-type leaves are unknown. In the same Permian layers in which *Sphenozamites rochei* occurs there are some stems and fructifications which may well belong to that species. The stems have the peculiar wood-structure typical of *Cycadoxylon* [RENAULT, 61; SCOTT, 69], and the fructifications were named *Cycadospadix milleryensis*. While there are no grounds whatsoever for assigning them to *Sphenozamites*, there is little doubt that they represent parts of cycadophyte plants. COMPTER also found associated structures rather like stone-fruits in the beds where *Sphenozamites tener* occurred, and thought that they may have belonged to that species [8]. ZEILLER doubted this and in a later publication COMPTER [9] agreed that the connection was not proved [LINELL, 48].

SPHENOZAMITES ROSSII ZIGNO emend.

Plate II, figs. 1-4; Plate III, fig. 1.

Text-fig. 4 A-E; Text-fig. 5 A-H; Text-fig. 6 A-B;
Text-fig 7 A-G; Text-fig. 8 A-B; Text-fig. 9 A-E.

1852. *Otozamites Rossii* - DE ZIGNO [86], p. 10. *Nomen nudum.*
1852. *Otozamites lanceolatus* - DE ZIGNO [86], p. 10. *Nomen nudum.*
1852. *Otozamites dentatus* - DE ZIGNO [86], p. 10. *Nomen nudum.*
1852. *Otozamites asplenioides* - DE ZIGNO [86], p. 10. *Nomen nudum.*
1868. *Sphenozamites Rossii* - DE ZIGNO [87], p. 14; fig. 9.
1870-72. *Sphenozamites Rossii* ZIG. - SCHIMPER [66], p. 162.
1870-72. *Sphenozamites latifolius* (BRONGN.) SAP. - SCHIMPER [66], p. 162 (ex parte); Pl. LXX, fig. 1 (reversed drawing of the Type-specimen of *Sphenozamites rossii*).
1875. *Sphenozamites Rossii* ZIG. - SAPORTA [63], p. 191; Pl. CXIV, figs. 1 (?) and 2.
1881. *Sphenozamites Rossii* ZIG. - DE ZIGNO [88, livr. 2-3], p. 114; Tab. XL, figs. 5-6.
1881. *Sphenozamites lanceolatus* - DE ZIGNO [88, livr. 2-3], p. 112; Tab. XXXIX, figs. 3-5.
1881. *Sphenozamites adiantifolius* - DE ZIGNO [88, livr. 2-3], p. 113; Tab. XL, figs. 1-4.
1900. *Sphenozamites Rossii* ZIG. - ZEILLER [85]; fig. 159.
1913 ?. *Sphenozamites Rossii* ZIG. - GRANDORI, Riassunto di Laurea. Name in list.

Type-specimen: DE ZIGNO [87]; fig. 9: DE ZIGNO [88]; Tab. XL, fig. 5. De Zigno Collection No. 4453.

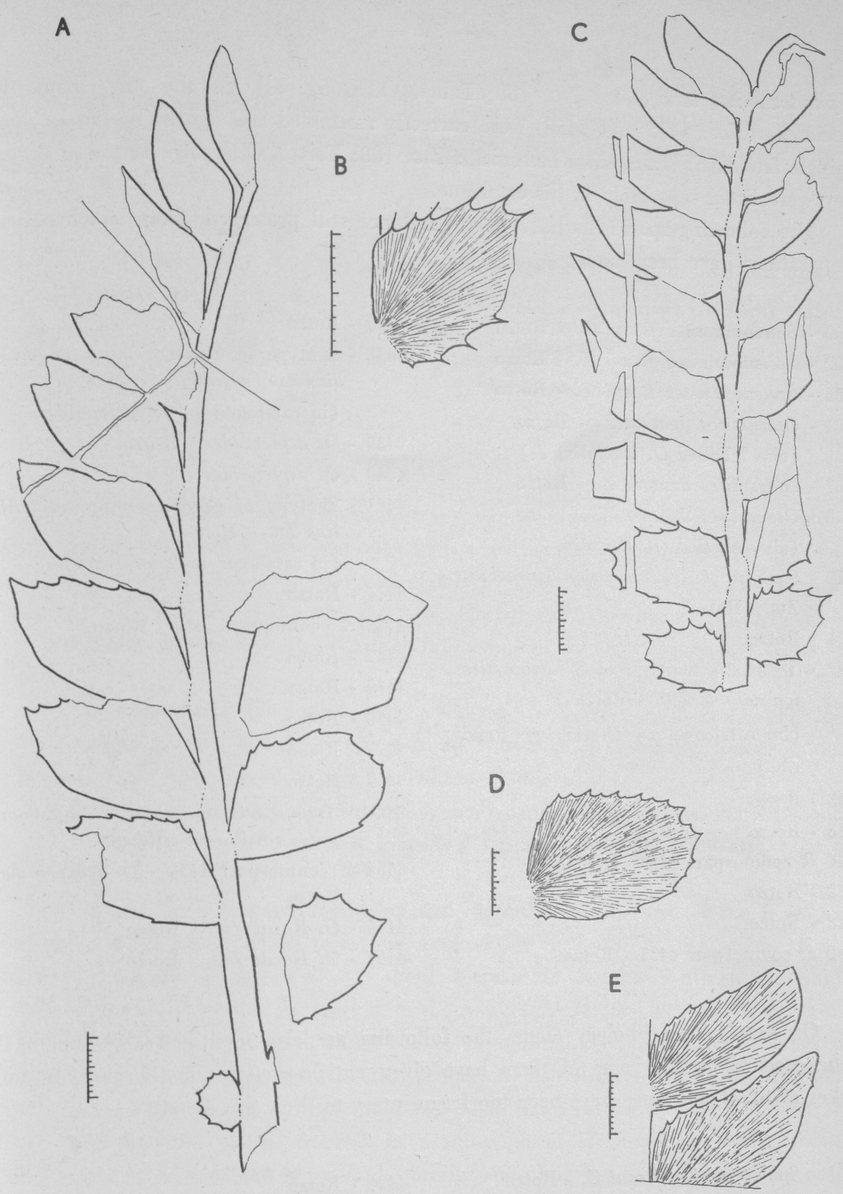
Locality: Rotzo.

Emended Diagnosis: Frond openly pinnate, oblong-lanceolate, up to 260.0 mm. long and 70.0 mm. broad in middle region, narrowing towards base and apex; rachis thick, rounded, longitudinally striated; pinnae alternate, with wedge-shaped bases, inserted obliquely on sides of rachis, remote in basal region, usually remote in middle and terminal regions, but occasionally approximate with margins slightly overlapping; basal pinnae smallest, orbicular or broadly triangular-obtuse, diverging at an angle of about 70° from rachis, margins spinulose-dentate; median pinnae largest, spreading, obliquely rhomboid-lanceolate, diverging at an angle of 50-60° from rachis, apices acute, proximal margins rounded, distal margins obtusely angled, both irregularly spinulose-serrate in more basal region of frond, becoming less incised and eventually entire towards terminal region; terminal pinnae smaller, narrower, more lanceolate-falcate, diverging at an angle of about 45° from rachis, apices acute, margins entire. Veins numerous, slender, dichotomous, radiating towards margins and apices; outermost acroscopic veins parallel with basal acroscopic edges of pinnae. Abaxial (?) cuticle of rachis thick: epidermal cells rectangular or squarish, typically 45 μ long x 28 μ wide (range 37 - 56 μ long; 18 - 37 μ wide); anticlinal walls about 4 μ thick, transverse straight, longitudinal wavy or straight, all without pits; outer surfaces flat, not sculptured, no papillae or trichome-bases present: stomata rare, sunken; guard cells crescent-shaped about 30 μ long, subsidiary cells two, lateral, unspecialised, without papillae or noticeable thickenings: hypodermal cells cutinised, rectangular, up to 93 μ long x 22 μ wide (range 18 - 30 μ); anticlinal walls minutely wavy, end walls truncate or sloping. Upper cuticle of pinna lacking stomata and trichome-bases, veins not indicated: cells more or less square about 42 μ long x 42 μ wide (range 27 - 56 μ); anticlinal walls 2 - 3 μ thick, distorted into rather deep narrow parallel-sided loops; outer surfaces smooth. Lower cuticle of pinna showing rather well-defined stomatal and non-stomatal bands, except

near edge of lamina where stomatal bands die out; stomatal bands 2 - 6 cells wide, not sunken, separated by 4 - 6 rows of ordinary epidermal cells: epidermal cells of non-stomatal band rectangular or irregularly square, typically 57 μ long x 27 μ wide (range 37 - 74 μ long; 8 - 44 μ wide), those of stomatal band usually shorter, more nearly square; anticlinal walls 1 μ thick, distorted into rounded loops of irregular length; outer surfaces smooth; occasional cells represent trichome-bases, with anticlinal walls much less sinuous or almost straight, and outer surfaces showing thinly cutinised central region surrounded by an increasingly more heavily cutinised part extending to anticlinal walls: stomatal bands consisting of stomata arranged in fairly well-defined rows, typically separated by 1 - 4 ordinary epidermal cells; rows not sunken; stomata sometimes adjacent within the row, but never sharing a common subsidiary cell and usually separated by one or more ordinary epidermal cells; occasional stomata occurring out of line; most stomata orientated transversely, very occasional ones obliquely: stomatal apparatus syndetocheilic, typically (including subsidiary cells) 55 μ long x 44 μ wide (range 48 - 74 μ long; 37 - 48 μ wide); guard cells sunken in shallow pit formed by two lateral subsidiary cells: subsidiary cells small, elongated; outer anticlinal walls straight or slightly bulging, thick, polar anticlinal walls much thinner; each subsidiary cell bearing a large papilla projecting over exposed surface of guard cell; papillae hollow, never meeting, with heavily cutinised walls; opening of stomatal pit hour-glass shaped, shorter than guard cells which are thus slightly overlapped by lip-like overhang of epidermal cells at poles: each guard cell about 44 μ long (range 37 - 48 μ), very broad in middle, abruptly narrowing towards poles; pore about 17 μ long (range 14 - 19 μ), situated at bottom of a shallow rectangular depression formed by the slightly thickened downwardly sloping part of inner walls of guard cells; depression delimited by rim of cuticle which is continued as a short sharp point at each end of pore; polar regions appearing clear and without cutinisation except for delicate line indicating line of contact between guard cells; upper wall with more intense thickening continuous from rim of depression through outer wall and into part of lower wall; thickening of upper wall plano-convex in surface view, very often with a polar peg-like projection at each end; thickening of lower wall concavo-convex, about half the width of upper thickening, becoming less intense towards its sharp concave limit.

Description: *Sphenozamites rossii* is represented by nearly forty specimens in the collection at Padua. All were collected at Rotzo and are preserved in the dark grey limestone typical of that locality. Only one specimen, which I doubtfully regard as belonging to this species, was collected elsewhere - No. 4442, from Scandolara. Every specimen is in the form of a compression and, in most cases, each has plant-substance and cuticle still preserved.

A careful examination of all the pieces of rock has enabled me to piece together several complete, or almost complete, fronds from separately numbered and catalogued specimens. For example, the Type-specimen proper, No. 4453 [87; fig. 9: 88; Tab. XL, fig. 5], is the larger, basal part of a frond which is also preserved on specimen No. 4400. This latter specimen has never been figured before and is now illustrated for the first time (Text-fig. 4 A; three uppermost pinnae). Similarly specimen No. 4457 (not figured previously) is the basal portion of the frond represented on No. 4410



TEXT-FIG. 4. *Sphenozamites rossii* ZIG.

A. Type-specimen Nos. 4400/4453; the three uppermost pinnae (No. 4400) are figured here for the first time; the remaining part is the Type-specimen proper and it is also shown in Plate II, fig. 1; Type-specimen proper figured twice by DE ZIGNO [87; fig. 9: 88; Tab. XL, fig. 5]. Scale equals 10.0 mm.

B. Basal pinna of specimen No. 4436; the pattern of venation and concentration of veins are approximately correct. Scale equals 10.0 mm.

C. Specimen No. 4441 shown also in Plate II, figs. 2 and 4; figured by DE ZIGNO as a syntype of *Sphenozamites adiantifolius* ZIG. [88; Tab. XL, fig. 1]. Scale equals 10.0 mm.

D. Specimen No. 4459; isolated pinna of the lower mid-region of a frond showing an approximately correct representation of the pattern of venation and concentration of veins; this pinna is also figured in Plate II, fig. 3. Scale equals 10.0 mm.

E. Specimen No. 4418; part of the mid-region of the frond showing pinnae with unequally denticulate margins; the pattern of venation and concentration of veins are approximately correct. Scale equals 10.0 mm.

(*Sphenozamites lanceolatus* Zig. [88; Tab. XXXIX, fig. 3]). On the other hand, two specimens (Nos. 4412 and 4458) were correctly assembled and figured by De Zigno as a single frond (*Sphenozamites lanceolatus* Zig. [88; Tab. XXXIX, fig. 4]), even though they were listed separately in his catalogue.

The following specimens have plant-substance still preserved, from which cuticle-preparations have been made:

4400 - *Sphenozamites Beani* Z. - Rotzo
4402 - *Sphenozamites Beani* Z. - Rotzo
4403 - *Sphenozamites Beani* Z. - Rotzo
4404 - *Otozamites dentata* Z. - Rotzo
(also labelled *O. ilicifolius* Z.)
4407 - *Otozamites dentata* Z. - Rotzo
4408 - *Otozamites dentata* Z. - Rotzo
(also labelled *O. ilicifolius* Z.)
4410 - Syntype of *Sphenozamites lanceolatus* Zig. - Rotzo
4411 - Rotzo
4412 with 4458 - Syntype of *Sphenozamites lanceolatus* Zig. - Rotzo
(in catalogue as *Otozamites Rossii* Zig.)
4413 - Rotzo
4415 - Rotzo
4416 & counterpart 4418 - Rotzo
4422 - Rotzo
4428 - Rotzo
4432 & counterpart 4433 - Rotzo
4435 - Rotzo
4438 - Syntype of *Sphenozamites adiantifolius* Zig. - Rotzo
(in catalogue as *O. asplenoides*)
4439 - *O. asplenoides* - Rotzo
4440 - *O. asplenoides* - Rotzo
4441 - Syntype of *Sphenozamites adiantifolius* Zig. - Rotzo
(in catalogue as *O. asplenoides*)
4444 - Rotzo
4445 & counterpart 4446 - Rotzo
4447 - Rotzo
4448 - Rotzo
4450 - Rotzo
4451 - Rotzo
4452 - Rotzo
4453 - Type-specimen proper of *Sphenozamites rossii* Zig. - Rotzo
4454 & counterpart 4455 - *O. lanceolatus* - Rotzo
4456 - *O. Rossii* Zig. - Rotzo
4457 - *O. Rossii* Zig. - Rotzo

On external morphology alone, the following are also identified as belonging to *Sphenozamites rossii*. Some of them have given cuticle-preparations, but the minute flakes of plant-substance have been too fragmentary to show any details:

4401 - *Sphenozamites Beani* Z. - Rotzo
4405 - *Otozamites dentata* Z. - Rotzo
(also labelled *O. ilicifolius* Z.)
4406 - *Otozamites dentata* Z. - Rotzo
(also labelled *O. ilicifolius* Z.)
4409 - *Otozamites dentata* Z. - Rotzo
(also labelled *O. ilicifolius* Z.)
4414 & counterpart 4425 - *O. Rossii* Zig. - Rotzo
4417 - Rotzo
4419 & counterpart 4420 - Rotzo
4421 & counterpart 4423 - Rotzo
4424 - Rotzo
4426 - Rotzo
4427 & counterpart 4429 - Rotzo
4430 & counterpart 4431 - Rotzo
4434 - Rotzo
4436 - Rotzo
4437 - Rotzo
4442 - Scandolara
4443 - Rotzo
4449 & counterpart 4461 - *O. Rossii* Zig. - Rotzo
4459 - *O. Rossii* Zig. - Rotzo
4460 - *O. Rossii* Zig. - Rotzo

To avoid confusion in these two lists some of the counterparts have not been indicated nor have some of the re-assembled fronds. These are now noted separately as follows:

4400 4453 - no counterpart
4401 - counterpart 4406
4402 4451 - counterpart (of both) 4452
4407 - counterpart 4408
4410 4457 - counterpart (of both) 4411
4412 4458 - counterpart (of both) 4413
4415 4450 - counterpart (of both) 4435
4438 - counterpart 4439
4440 - counterpart 4441
4447 4448 - no counterpart

The pinnate fronds of *Sphenozamites rossii* are typically oblong-lanceolate in outline, narrowing towards base and apex with a corresponding diminution in size of the pinnae. The largest frond (No. 4454 and counterpart No. 4455) measures 260.0 mm. in length and is 53.0 mm. at the broadest part. Twenty-three pinnae are preserved, but there are traces of others indicating that the complete frond probably had twenty-six (Text-fig. 5 C).

The Type-specimen (including both pieces of rock, Nos. 4453 and 4400) lacks several terminal pinnae, but the complete frond is calculated as having measured about 210.0 mm. long. At its broadest part it measures 72.0 mm.

The rachis is robust and rounded and typically, in large specimens, measures about 6.0 mm. in diameter at the base, with a gradual taper to about 1.5 - 2.0 mm. near the end.

The pinnae are alternately arranged and, according to the size of the frond, are about 8.0 - 15.0 mm. distant from one another on each side of the rachis at their insertions. Each frond shows a very slight decrease in distance between the pinnae towards the terminal region. In most cases the pinnae are remote throughout the frond, but occasional specimens show them somewhat approximate, especially towards the terminal region where the margins of such pinnae overlap slightly (specimen No. 4441, Text-fig. 4 C; Plate II, fig. 4). Specimen No. 4417 is interesting in that it is part of a frond which had the pinnae inserted in a sub-opposite arrangement. Each pinna is wedge-shaped at its base and is inserted laterally and obliquely on the side of the rachis which is thus not hidden by the bases of the pinnae. The lowermost pinnae diverge at an angle of about 70° from the rachis and the terminal pinnae at 45°, the intermediate pinnae showing a gradual change in angle of divergence. Measurements have been made on as many specimens as possible and this observation holds good for all of them.

The pinnae of the lowermost part of a frond are the smallest, rounded or broadly triangular-obtuse in shape, with the margins coarsely dentate all round with each tooth prolonged into a spine. Towards the median region of the frond the pinnae are much larger and gradually assume an obliquely rhomboid-lanceolate form. The largest median pinna of the Type-specimen is 36.0 mm. long and 20.0 mm. broad, but the maximum dimensions for a leaflet in this part of a frond are recorded from specimen Nos. 4447/4448 which has a pinna measuring 42.0 mm. in length and 23.0 mm. in breadth.

A characteristic feature of these median pinnae, as well as of the terminal pinnae, is the distinctly obtusely-angled distal margin (Text-fig. 4 A). All the median pinnae have acute apices. The more basal pinnae of the middle region have irregularly serrate margins with the serrations ending in spines. There is a transition in this middle region, from those more basal pinnae with this type of margin, through forms which have much shorter spines, to the more terminal ones with entire margins which are entirely devoid of spines and serrations. The terminal pinnae are more splender and lanceolate-falcate in outline, with acute apices and entire margins.

The veins are numerous and slender, bifurcating several times as they run fan-wise from the insertion towards the margin and apex of a pinna. A constant and characteristic feature is the manner in which the outermost acroscopic veins always run parallel with the basal part of the distal margin of a pinna, and are not foreshortened as those in the basiscopic position (Text-fig. 4 B, D and E).

From their size and form, two very small specimens are considered to be fronds of young plants (Text-fig. 5 D and H). The smaller, No. 4405, has only six pinnae, of which the basal ones are the largest. Four of the pinnae have spiny margins similar to those of the basal pinnae of large fronds. The larger specimen, No. 4404, had thirteen pinnae, of which the basal ones are also the largest. These are much like the basal pinnae of a large frond and have similar spiny margins. The terminal pinnae are smaller and lanceolate in shape with entire margins and acuminate apices. Both specimens show a narrowing of the frond-outline only towards the apex. It should also be noticed that the rachis is rather broad in relation to the size of the pinnae, especially at the base of the specimens. Three other small specimens (Nos. 4401, 4408 and its counterpart No. 4407) are incomplete and represent the terminal regions of two slightly older and larger fronds than those just described (Text-fig. 5 B and E).

Remarkably well-preserved cuticle has been obtained from a large number of specimens in the De Zigno Collection and it has been possible to make a relatively complete study of the microscopic characters of the epidermis of *Sphenozamites rossii*. In addition to cuticle obtained from both the upper and lower surfaces of pinnae, some large pieces of cuticle have also been prepared from the rachis of specimen No. 4432. Considerable detail is shown, but it is not known to which surface of the rachis these fragments belong, though the presence of a few stomata suggests the lower surface.

TEXT-FIG. 5. *Sphenozamites rossii* ZIG. →

A. Syntype of *Sphenozamites lanceolatus* ZIG. [88; Tab. XXXIX, fig. 4] shown also in Plate III, fig. 1; upper part is specimen No. 4412, lower part is specimen No. 4458. Scale equals 10.0 mm.

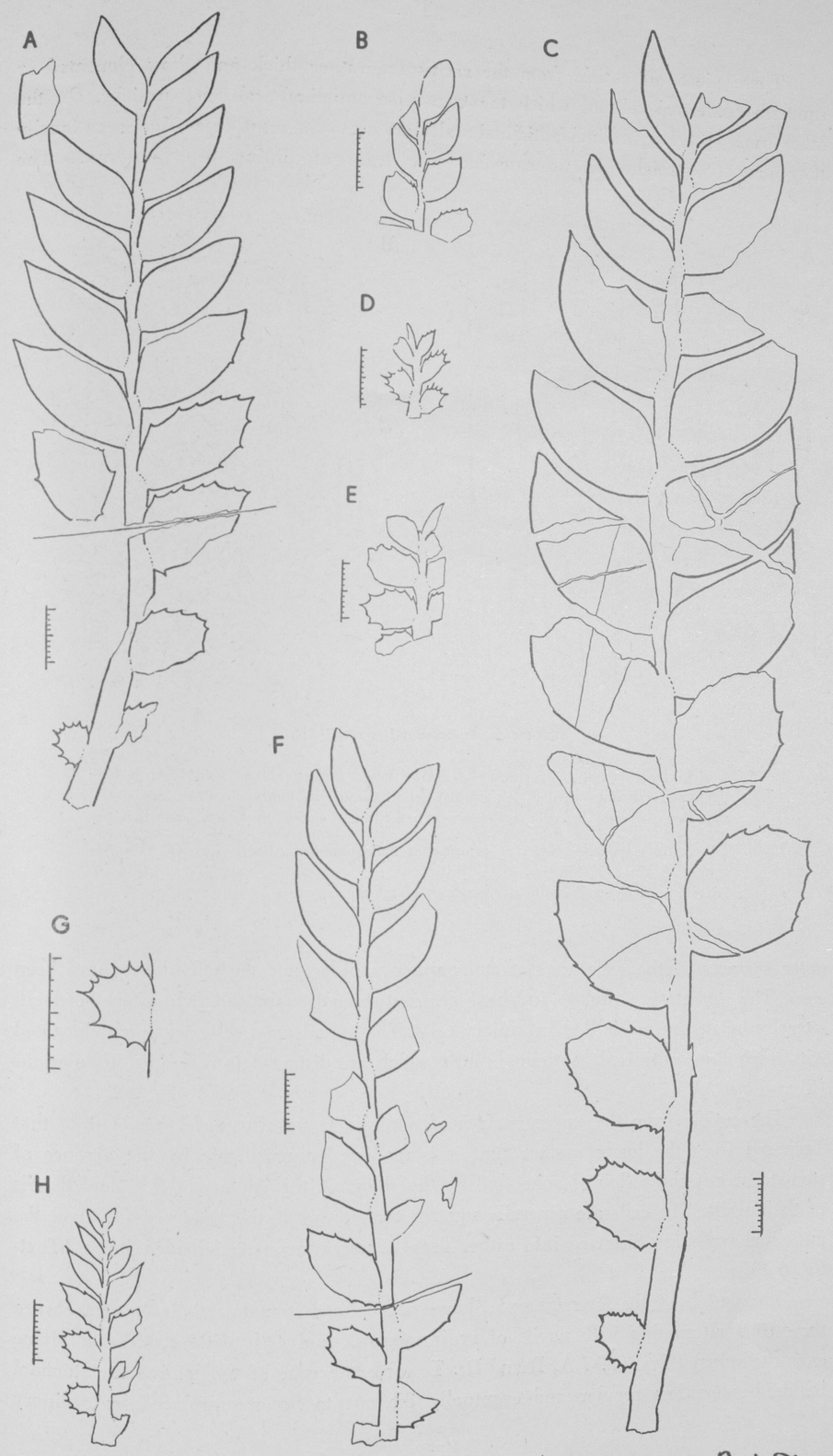
B and E. Apical parts of two juvenile fronds; specimen No. 4401 (B), specimen No. 4408 (E). Each scale represents 10.0 mm.

C. Specimen No. 4455. Scale equals 10.0 mm.

D and H. Two complete juvenile fronds; specimen No. 4405 (D), specimen No. 4404 (H). Each scale represents 10.0 mm.

F. Specimen Nos. 4410/4457; the lower part (No. 4457) is figured here for the first time; the remaining part is specimen No. 4410 and it was figured by DE ZIGNO as a syntype of *Sphenozamites lanceolatus* ZIG. [88; Tab. XXXIX, fig. 3]. Scale equals 10.0 mm.

G. Lowermost pinna of specimen No. 4458 (figured in A, above). Scale equals 10.0 mm.



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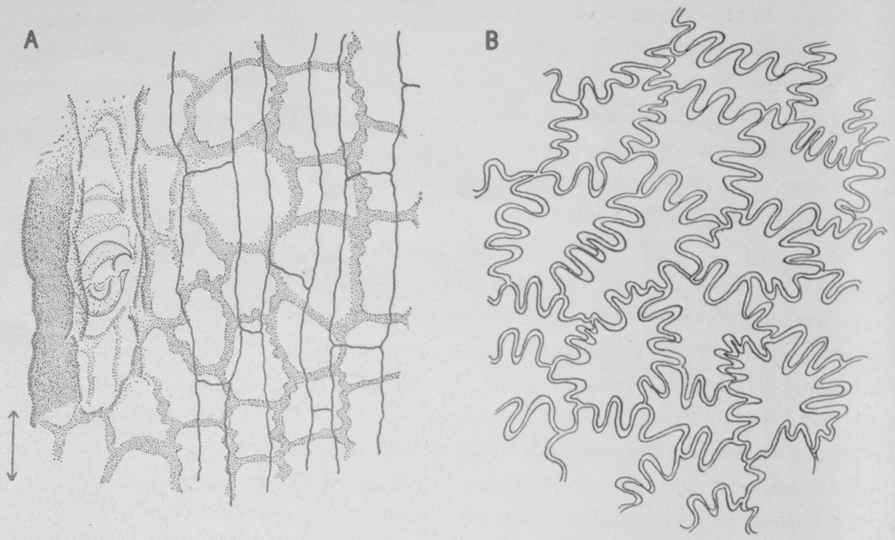
These pieces of cuticle from the rachis are rather thick and show elongated or squarish epidermal cells of which the transverse anticlinal walls are straight. On the other hand, the longitudinal anticlinal walls are wavy in most cases, but occasionally they may be straight. In no case has any trace of pitting been observed. The



TEXT-FIG. 6. *Sphenozamites rossii* ZIG.

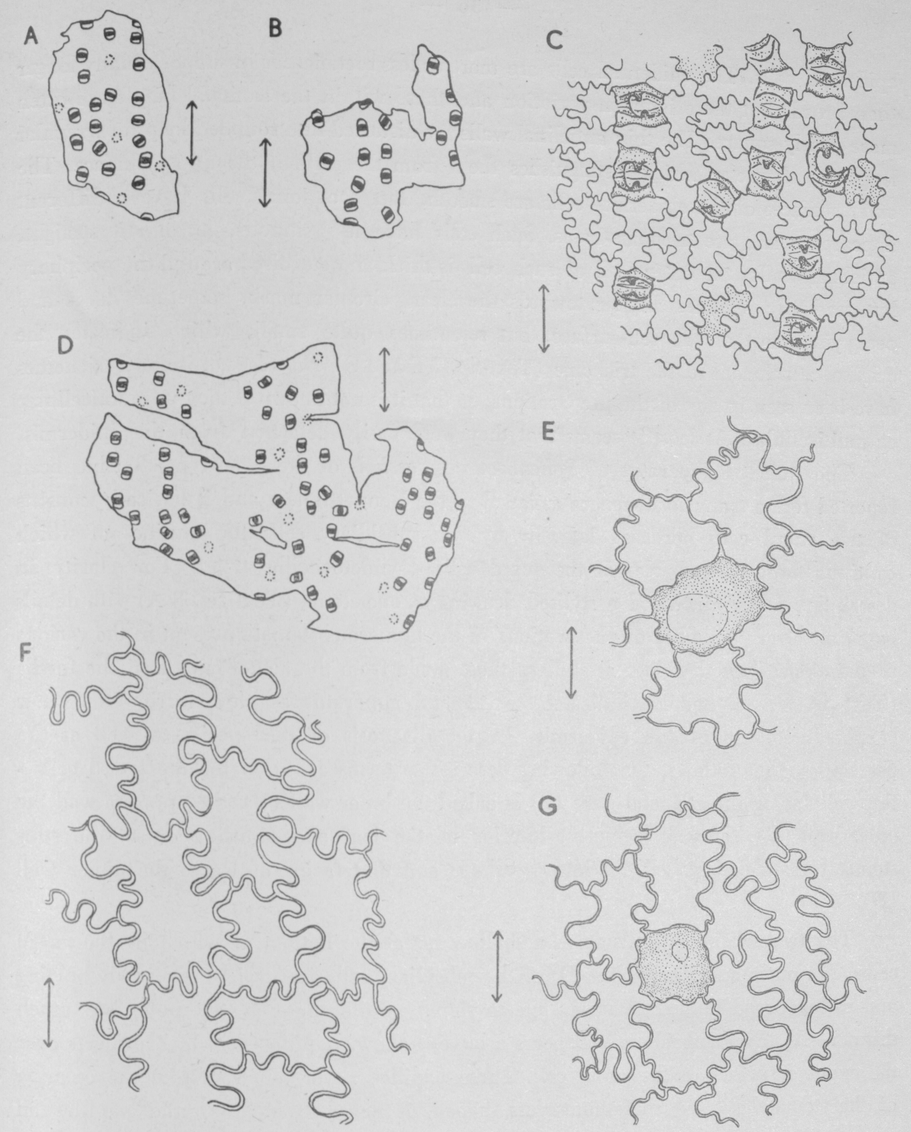
A. Cuticle from rachis of specimen No. 4432; lower surface (?) as seen from inside; epidermal-cell walls stippled, hypodermal cells indicated by unbroken lines; one stoma, with characteristic guard cells, is shown next to the fold of cuticle on the left; slide B. X 400.

B. Cuticle from specimen No. 4441 (syntype of *Sphenozamites adiantifolius* ZIG.); upper surface of pinna. X 400.
(Arrow in A is parallel with the long axis of the rachis).

outer surfaces of the cells are flat and neither papillae nor trichome-bases have been seen. The stomata are sunken and have crescent-shaped guard cells which are bordered laterally by two unspecialised subsidiary cells. The hypodermal cells are much elongated with very fine, cutinised, anticlinal walls which are distorted into minute undulations (Text-fig. 6 A).

The cuticle from the upper surface of a pinna is usually more fragile than that prepared from the lower surface, but it is readily distinguishable by the absence of stomata or any indication of veins and by the shape of the epidermal cells and details of their walls. The cells are generally squarer than those of the lower surface and the anticlinal walls are distorted into rather deeper, narrower, parallel-sided loops (Text-fig. 6 B).

The cuticle of the lower surface shows well-defined stomatal bands (lying between the veins) alternating with bands of ordinary epidermal cells without stomata (lying over the veins) (Text-fig. 7 A, B and D). Towards the edge of the lamina the stomatal bands become less regular and eventually die out to become replaced by ordinary



TEXT-FIG. 7. *Sphenozamites rossii* ZIG.

A, B. Cuticle from Type-specimen proper No. 4453; lower surface of pinna showing distribution of stomata and trichome bases; guard cells and orientation of pores indicated by heavy black lines, trichome bases shown as dotted circles; A, slide A; B, slide B. X 50.

C. Cuticle from the lower surface of a pinna of the Type-specimen proper showing stomata and trichome bases; slide B. X 160.

D. Cuticle from the lower surface of a pinna of specimen No. 4438 (syntype of *Sphenozamites adiantifolius* ZIG.); guard cells and orientation of pores indicated by heavy black lines, trichome bases shown as dotted circles. X 50.

E. Cuticle from the lower surface of a pinna of specimen Nos. 4412/4458 (syntype of *Sphenozamites lanceolatus* ZIG.) showing epidermal cells and one trichome base; slide A. X 400.

F. Cuticle from the lower surface of a pinna of the Type-specimen proper showing epidermal cells in the region between two stomatal bands; slide A. X 400.

G. Cuticle from the lower surface ot a pinna of specimen No. 4432 showing epidermal cells and one trichome base; slide A. X 400.
(Arrows indicate direction of stomatal rows).

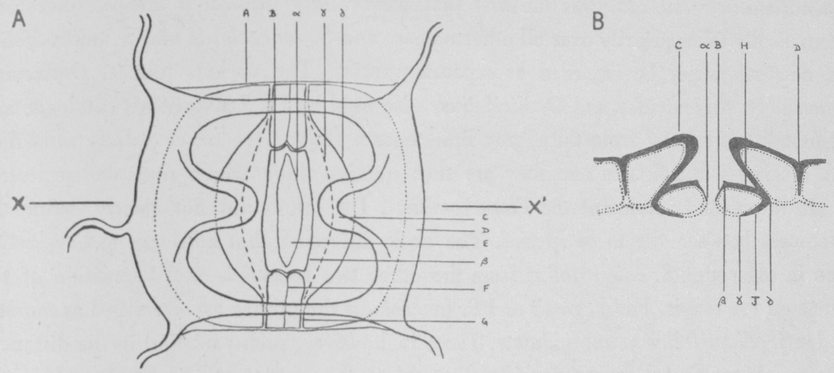
epidermal cells. The epidermal cells are more or less rectangular in shape, usually longer than broad, but there is much variation and those within the stomatal bands are often more nearly square. The thin anticlinal walls are distorted into rounded loops of irregular length, a character which distinguishes them from the cells of the upper surface. The outer surfaces of the epidermal cells are smooth, but occasional cells have a different appearance and are trichome-bases. Such cells have less sinuous, or almost straight, anticlinal walls; the outer wall of such cells is thick and cutinised around the periphery but gradually becomes thinner towards the clear, circular mark, sometimes large and occupying most of the cell-surface, but sometimes quite small, which indicates the original attachment of the trichome (Text-fig. 7 E and G). No traces of isolated trichomes have been seen in any of the preparations, so that it is not known if they were unicellular or multicellular. At least it seems that they were easily detached from the epidermis.

The stomatal apparatus of *Sphenozamites rossii* is of the same type that has been reported for so many form-genera assigned to the Bennettitales, and it basically consists of two guard cells bordered laterally by two subsidiary cells the outlines of which continue those of the poles of the guard cells (syndetocheilic type). For clarity in description I have included a stylised drawing of one stoma (Text-fig. 8 A) with details based on a large number of observations of the numerous stomata present in the various preparations. This drawing, as well as those made from the actual cuticle of the fossils (Text-fig. 9 A, D and E), indicates the stomatal apparatus as viewed from the outer (exposed) surface of the epidermis. In the diagnosis of the species as well as the description that follows, the following descriptive terms are used for the guard cells - the wall facing the stomatal pore (E) is called the inner wall (B), the opposite wall the outer wall (δ); the wall facing the interior of the leaf and abutting on to the sub-stomatal chamber is called tthe lower wall (J) and that facing outwards the upper wall (H).

The two subsidiary cells form a shallow pit at the bottom of which lie the guard cells. The outer anticlinal walls (D) of the subsidiary cells are straight or slightly bulging and rather broad in surface view (due to slope), while those at the poles are much thinner (A). Each subsidiary cell bears a large, hollow, papilla (C) which projects over the exposed surface of the guard cell. These papillae never touch so that the opening of the stomatal pit, which is hour-glass shaped, is never divided. Similar papillae on the subsidiary cells are recorded in species of *Ptilophyllum* [Harris, 28, 31; Jacob & Jacob, 38]. The actual opening is slightly shorter than the guard cells, which are slightly overarched at their poles by a lip formed by the walls of the polar epidermal cells.

The guard cells are very broad in their mid-region but become abruptly much narrower towards their poles. The cutinised lamellae are very distinct and constant in their position and form. The cutinised parts of the inner walls (B) of the guard cells slope down and become gradually thinner towards the pore so creating a rectangular depression at the bottom of which the actual pore is situated. The upper margin of this depression is delimited by a rim of cuticle (β) which is continued as a short sharp point at each and of the pore. The polar regions of the inner wall are clear (K) and apparently devoid of thickening, though a delicate cutinised line indicates the line of

contact (F) between the guard cells. The upper wall (H) of the guard cell is completely and much more intensely cutinised. The cutinised lamella is continuous outward from the rim of the depression and is plano-convex in surface view. At the poles it is very often continued as a peg-like projection (G) right to the end of the guard cell. The cutinised lamella of the lower wall (J) is concavo-convex (crescentic) in surface view and is continuous in the outer wall of the guard cell with that of the upper wall. There is thus a complete cutinisation in three walls of the guard cell. The cutinised lamella of the lower wall only extends about half way across the wall towards the pore, and it ends at a sharp rim along its concave limit. In the drawing of a stylised stoma this sharp rim is indicated by a broken line (Text-fig. 8 A γ), but in the drawings of



Text-fig. 8. *Sphenozamites rossii* Zic.

A. Stylised drawing of the surface view of a stomatal apparatus as seen from the outer surface.

B. Reconstructed transverse section through stomatal apparatus along the line X - X'.

EXPLANATION OF SYMBOLS

α - Edge of cuticle surrounding pore.
β - Rim of cuticle surrounding depression formed by downwardly sloping parts of the inner walls of the guard cells.
γ - Sharp rim at concave limit of thickening of lower wall of guard cell.
δ - Outer wall of guard cell.
A - Polar anticlinal wall of subsidiary cell.
B - Inner wall of guard cell.
C - Subsidiary-cell papilla.
D - Outer anticlinal wall of subsidiary cell.
E - Pore.
F - Line of contact between guard cells.
G - Polar peg-like continuation of thickening of upper wall of guard cell.
H - Upper wall of guard cell.
J - Lower wall of guard cell.
K - Clear polar region of inner wall of guard cell.

actual stomata it is represented by a continuous line (Text-fig. 9 A, C, D and E). Much time was spent in elucidating the nature of the cutinised lamella of the lower wall for, at first, it was thought that the sharply defined rim might represent the line of contact between the upper wall of the guard cell and its adjacent subsidiary cell. When viewed from the outer surface it corresponds in position with such a line of junction as has so often been figured in drawings of bennettitalean stomata [Harris, 28; 29; 31; 32; 34; Jacob & Jacob, 38]. However, careful examination of many examples has shown that this sharp rim is actually at a much lower level of focus when seen in stomata viewed from outside, and at the highest level of focus when seen in stomata viewed from inside. Finally, I believe that this interpretation is proved beyond doubt when reference is made to the drawing of a stomata viewed from inside (Text-fig. 9 C).

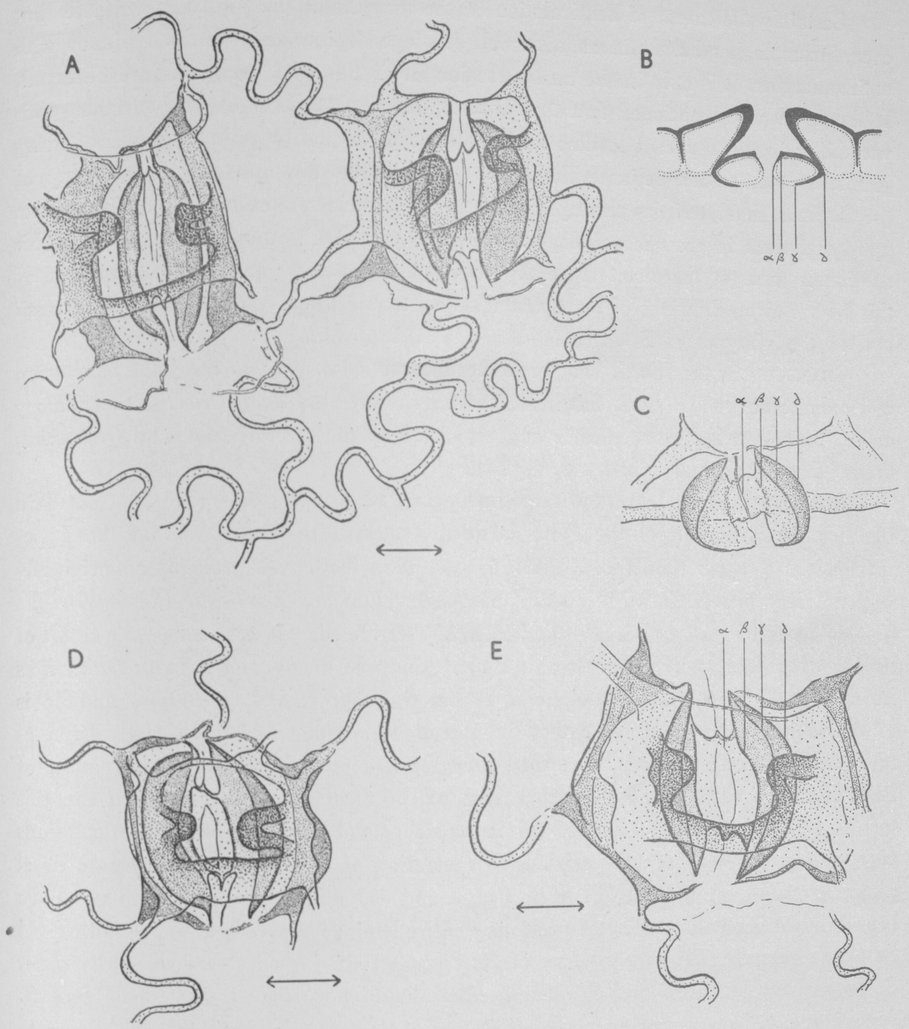
Discussion and Comparison: - *Sphenozamites rossii* was first described and illustrated by De Zigno in a paper which incuded the first descriptions and figures of some species of *Otozamites* that had also been collected from the « grey limestones » of Veneto [87]. The species was re-described in the first volume of the *Flora fossilis*...., when two additional and very similar species, *S. lanceolatus* Zig. and *S. adiantifolius* Zig. were described and figured for the first time [De Zigno, 88].

A survey of all the specimens assigned by De Zigno to these three species, together with an examination of the cuticle from the specimens from which it could be prepared, has led me to regard all three as representing a single species, *Sphenozamites rossii*. The differences that occur between one frond and another can only be regarded as morphological variations and not of valid specific significance. The specific designation *Sphenozamites rossii* Zig. was the first that was validly published and it, therefore, automatically takes priority over all other names, and *S. lanceolatus* and *S. adiantifolius* can now no longer be regarded as separate species. The various names, *Otozamites dentatus*, *O. asplenioides* and *O. ilicifolius*, also used by De Zigno in his catalogue and the first list of species from the « grey limestones » [86], were never validly published with diagnoses and figures and they are thus *nomina nuda* which must be neglected.

In the second volume of the *Flora fossilis*... De Zigno did not clearly define the differences between the three species. The basic difference that he seems to have relied upon in separating *S. adiantifolius* from the other two species is the disposition of the pinnae on the rachis. For *S. rossii* and *S. lanceolatus* the pinnae are described as remote, but for *S. adiantifolius* as approximate. There is, however, such variation in the distances between pinnae that I cannot consider that this was a sufficiently important character for the institution of a separate species. In general, the pinnae are remote, but some fronds show the pinnae to be somewhat approximate towards the terminal region. Even the Type-specimen proper of *S. rossii* has the margins of some adjacent pinnae slightly overlapping (Text-fig. 4 A; Plate II, fig. 1).

De Zigno gives no comparison between *S. adiantifolius* and *S. rossii*, but in the description of *S. lanceolatus* there is a note indicating how that species differs from both *S. geylerianus* and *S. adiantifolius*. He writes: « Questa specie (i. e. *S. lanceolatus*) presenta una forma che dir si potrebbe intermedia fra quella descritta sotto il nome di *Sphenozamites Geylerianus*, e quella di cui segue le descrizione col nome di *Sphenozamites adiantifolius*. Si distingue però dalla prima per avere le pinne più ampie, di forma lanceolata e coll'apice acuto, e dalla seconda, oltre che per la diversa forma delle pinne, per la mancanza delle denticolazioni del margine, che formano uno dei caratteri principali di quest'ultima ».

De Zigno was correct in distinguishing *S. lanceolatus* from *S. geylerianus* on the shape of the pinnae and the form of their apices - in *S. geylerianus* the pinnae are obliquely oblong-lanceolate with obtuse apices and they always have entire margins. But his statement that *S. lanceolatus* is distinguished from *S. adiantifolius*, because it lacks the characteristic denticulation of the margins of the pinnae of *S. adiantifolius*, is entirely incorrect and also contradictory to what precedes in both the latin diagnosis and italian description of *S. lanceolatus* where he writes « *marginibus denticulatis* » and « margini denticolati » referring in both cases to the basal pinnae.



Text-fig. 9. *Sphenozamites rossii* Zig.

A. Two stomata from the lower surface of a pinna of the Type-specimen proper No. 4453; slide B. X 700.

B. Reconstructed transverse section through stomatal apparatus at right-angles to pore; cutinised walls shown black, uncutinised walls dotted.

C. Folded cuticle from specimen Nos. 4412/4458 (syntype of *Sphenozamites lanceolatus* Zig.) showing details of guard-cell thickenings as seen from below (inside); slide A. X 700.

D. Stomatal apparatus from the lower surface of a pinna of specimen Nos. 4412/4458 (syntype of *Sphenozamites lanceolatus* Zig.); slide B. X 700.

E. Stomatal apparatus from the lower surface of a pinna of specimen No. 4441 (syntype of *Sphenozamites adiantifolius* Zig.); X 700.

(Arrows in A, D and E indicate direction of stomatal rows; explanation of greek letters in B, C and E as for Text-fig. 8).

Certainly the extent of denticulation of the margins of the pinnae is variable, but every example has basal pinnae with well-developed spines and terminal pinnae with entire margins. It is only in the median region of fronds that variations are observed. It should also be mentioned that the shape of the leaflets is somewhat variable. This variability in the shape of leaflets might well be paralleled by pinnate fronds of living plants, so that greater reliance should be placed upon the remarkable constancy of the defined characteristics throughout the many cuticle preparations examined than upon variations in gross morphology. I cannot accept De Zigno's distribution of his specimens amongst three not especially well-defined species, and in corroboration of this I have given drawings of the stomatal apparatus of the Type-specimen of *S. rossii* and of the syntypes of *S. lanceolatus* and *S. adiantifolius*.

Grandori, in the fourth chapter of her *Laurea*, also came to the same conclusion and only recognised *S. rossi*, but her observations were based on external morphology alone, while Seward went further and associated all the three species with *Otozamites beani* (L. & H.) Brongn. [Seward, 71; 74].

Seward examined De Zigno's specimens in Padua and, while there, he noted in his own personal copy of the *Flora fossilis....*, against the illustration of the Type-specimen of *S. rossii* [88; Tab. XL, fig. 5], that the « leaflet was probably not originally ragged - very like *O. Beani* », and in the third volume of his *Fossil Plants* [74] he writes that he was led « to regard the irregularly serrate edge of the pinnae as a result of tearing of an originally entire lamina and to compare the specimens with *Otozamites Beani* (L. & H.) ». Schuster also says that *S. rossii* recalls *Otozamites* and he is of the same opinion as Seward that the serrations are due to tearing [68]. Even as far as the Type-specimen is concerned Seward was mistaken as an examination of Plate II, fig. 1 will show. I agree that some of the median pinnae have their margins torn in places, but not all, and the two lower right-hand pinnae show the denticulations very clearly. In many other specimens this serration of the margins of the more basal pinnae is even more evident (Plate II, figs. 2 and 4), and it certainly could not have been brought about by tearing of previously entire laminae. We can, therefore, disregard Seward's remark [74] that all four of De Zigno's Italian species (i. e. *S. geylerianus*, *S. lanceolatus*, *S. rossii* and *S. adiantifolius*) should be assigned to a single type *S. geylerianus*. *S. geylerianus* is most definitely a distinct species, not only with regard to its external morphology as pointed out above, but also with regard to its cuticle which, though fragmentary, is different from that of *S. rossii*.

Saporta [63] regarded *Sphenozamites rossii* as a distinct species and re-figured the Type-specimen of De Zigno (No. 4453) on his Planche CXIV fig. 2. In addition, he also figured (Planche CXIV, fig. 1) an incomplete, isolated pinna from rocks of Lower Kimmeridgean age at Morestel (Isère). However, this particular pinna is damaged at the margins and apex and it is difficult to be certain to what extent there were denticulations along the margins. De Zigno [88] himself remarks upon this fact and considered that the pinna could not, with certainty, be assigned to *S. rossii*, and with him I agree. Indeed, Saporta was not certain either for he writes « il n'est pas bien certain, à notre sens, que l'exemplaire de Morestel soit spécifiquement identique avec ceux des Alpes vénitiennes. Il constitue au moins une forme dont l'analogie avec celle que Zigno a si bien décrite ne saurait être révoquée en doute ».

The drawings of *Sphenozamites latifolius* (Brongn.) Sap., in Schimper [66; Pl. LXX, figs. 2 and 2 b], which are the reverse (i. e. printed in such a manner as to look like counterparts of the originals) of those in Saporta [63; Pl. CXII, fig. 1 and Pl. CXIII, fig. 2], indicate that this species is distinct from *S. rossii*. *S. latifolius* is distinguished by possessing more broadly ovate or orbicular pinnae which are inserted transversely, perhaps by very short stalks, on the rachis. The pinnae are far more symmetric in shape than those of *S. rossii* and when detached show a sinus-like indentation with two short, sharp auricles suggesting that (in the living condition) the leaflet-attachments were slightly amplexicaul. In addition, the margins of the pinnae of *S. latifolius*, even though sinuous, are entire and devoid of spines.

Schimper [66] mistakenly figured the Type-specimen of *S. rossii* in a reversed position on his Planche LXX, fig. 1 as *S. latifolius* Sap. and says distinctly « d'après un dessin de M. Saporta », while Saporta described and illustrated the same specimen on his Planche CXIV, fig. 2 correctly as *S. rossii*. This fact seems only to have been noticed and commented upon previously by Feistmantel [12]. The specimen figured by Schimper may actually be the counterpart of the Type-specimen of *S. rossii*, *a* drawing of which may have been sent to him by Saporta. I do not know if such a counterpart ever existed - it is certainly not listed in De Zigno's catalogue nor is it to be found in his collection at Padua. It seems unlikely that De Zigno had given the counterpart to Saporta for the latter author says distinctly that his own illustration, which was not reversed in printing, is « d'après une figure empruntée au Memoire de De Zigno sur les Cycadées fossiles de l'Oolithe des Alpes vénitiennes ».

The much larger, isolated pinnae of *S. belli* Sew. [Seward, 72; 74] from the Stonesfield Slate of England, though compared by Seward with the species from Italy, are sufficiently distinct in their shape not to be identified with *S. rossii*.

No discussion of *Sphenozamites rossii* would be complete without some further reference to Seward's continued suggestions that it, together with the other Italian species *S. geylerianus*, should more correctly be compared with *Otozamites beani*. Perhaps the clue to Seward's line of thought is to be sought in De Zigno's own writings. In De Zigno's first paper on the fossil plants from the « grey limestones » [86] he lists *Otozamites beani*, amongst the « Piante fossili dell'Oolite di Monte Spitz. di Rotzo nei Sette Comuni del Vicentino », in addition to *Otozamites rossii*, *O. asplenoides*, *O dentatus* and *O. lanceolatus* which are now regarded as synonyms of *Sphenozamites rossii*.

Otozamites beani is not referred to in any of the later publications as occurring in the Italian Flora, though of course it is described in the second volume of the *Flora fossilis....* [88] as a typical British species. By the time this was written (1881), De Zigno had had more opportunity to study all his specimens and to reconsider his published list of 1852-53 [86]. His labels (where they still exist) and catalogue are of an early date and give many names which were changed when the actual specimens were described and figured. The label of specimen No. 4400 bears the name « *Sphenozamites beani* Z. » in De Zigno's handwriting, and amongst his manuscripts there is an early water-colour of the same specimen bearing the name « *Otozamites*

beani ». It is obvious that this specimen was the basis for including *Otozamites beani* in the first list of plants from Rotzo [86]. This is a very important specimen, however, for it represents three of the terminal pinnae of the Type-specimen proper (No. 4453) of *Sphenozamites rossii*. The original piece of rock must have become broken and the two pieces (each bearing part of the same fossil) separated at the time of collection, so that when they were eventually catalogued they acquired different names and non-consecutive numbers. These three pinnae show all the characters exhibited by pinnae in a similar position on other fronds of *S. rossii*, and I can distinguish no feature that could possibly merit their being identified with *Otozamites beani*. They do not show the typically auricled base of that species nor the rounded apex, and in addition the pinnae are attached laterally on the rachis and not on the upper side as in *O. beani*.

A comparison of the cuticles of *Sphenozamites rossii* and *Otozamites beani* is very instructive and points very clearly to their being two very distinct and different species. Apart from minor differences in epidermal-cell shape and dimensions, there is a very marked difference in their stomatal structure, even though it is basically of the syndetocheilic type. The shallow stomatal chamber of *S. rossii*, with its hour-glass shaped opening and large papillae on the subsidiary cells, is quite unlike the deep chamber of *O. beani* which opens to the surface by a very constricted lobed opening [Harris, 32].

SPHENOZAMITES GEYLERIANUS Zigno emend.

Plate III, figs. 2-3.
Text-fig. 10 A-E.

1881. *Sphenozamites Geylerianus* - De Zigno [88, livr. 2-3], p. 107; Tab. XXXIX, figs. 1-2.

Type-specimen: De Zigno [88]; Tab. XXXIX, figs. 1-2. De Zigno Collection No. 4399 (and counterpart No. 4388).

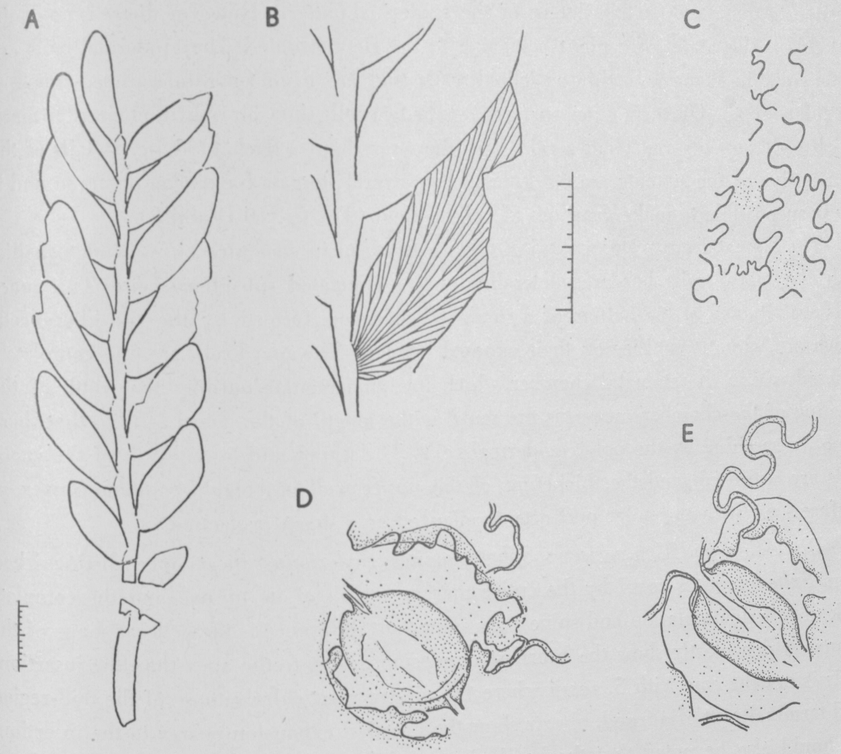
Locality: Valle Zulliani, near Roverè di Velo.

Emended Diagnosis: Frond openly pinnate, linear-oblong, more narrowed at base than apex; rachis thick, longitudinally striated; pinnae alternate, with wedge-shaped bases, inserted obliquely on sides of rachis, diverging at an angle of 35-40° from rachis, remote, obliquely oblong-elliptic, curving upwards a little towards their obtuse apices; margins entire. Veins numerous, slender, dichotomous, radiating towards margins and apices; outermost acroscopic veins parallel for a short distance with basal acroscopic edges of pinnae. Cuticle fragmentary; (distribution of stomata not known): epidermal cells rectangular, 44-63 μ long x 22 μ wide; anticlinal walls less than 1 μ thick, distorted into rounded loops of irregular length, outer surfaces with an indistinct circular mark (? papilla or trichome-base) 14 μ in diameter: stomatal apparatus syndetocheilic, about 45 μ long x 35 μ wide (including subsidiary cells); guard cells slightly sunken in shallow pit formed by two lateral subsidiary cells: subsidiary cells variable, elongated; outer anticlinal walls sinuous at surface level, bulging and rounded beneath; opening of stomatal chamber irregular in outline, same length as guard cells: guard cells 35 μ long,

elongated, very broad in middle, abruptly narrowing towards poles; pore about 14 μ long, situated at bottom of a shallow depression formed by the thinly cutinised inner walls of guard cells; upper wall of guard cell with a more intense thickening, irregularly plano-convex in surface view, very often with a polar peg-like projection at each end.

Description: Only the Type-specimen and counterpart of *Sphenozamites geylerianus* are known, but a similar, unlabelled specimen, No. 4170 from Roverè di Velo, is tentatively identified as belonging to the same species.

The pinnate frond is linear-oblong in shape and measures 30.0 mm. wide in its broadest region. The distal pinnae are lacking, but I agree with De Zigno [88] in calculating the original length of the frond at about 130.0 mm. The rachis is fairly robust and irregularly marked throughout its length with ribs and furrows which suggest that flattening of an originally rounded structure has taken place during the fossilisation process. At the base of the frond the rachis is about 4.0 mm. in diameter, and it is devoid of pinnae for the first sixteen millimetres of its length.



Text-fig. 10. *Sphenozamites geylerianus* Zig.

A. Type-specimen No. 4399 shown also in Plate III, figs. 2 3; figured by De Zigno [88; Tab. XXXIX, fig. 1]. Scale equals 10.0 mm.
B. Part of Type-specimen enlarged to show venation (drawn accurately). Scale equals 10.0 mm.
C. Epidermal cells from cuticle of Type-specimen. X 400.
D and E. Two stomata from separate fragments of cuticle from the Type-specimen. X 700.

Fourteen pinnae are preserved, those at the base and towards the tip of the frond being progressively somewhat smaller than those in the median region. The pinnae diverge at angles of about 35 - 40° from the rachis, and successive pinnae are about 10.0 mm. distant from one another on a side of the rachis. Towards the tip of the leaf the pinnae are slightly closer to one another, but throughout the length of the leaf they are always remote at their insertions, even though there is a tendency for the margins of the more terminal pinnae to overlap slightly. Each pinna is obliquely oblong-elliptic in shape and curved slightly upwards towards an obtuse apex, while towards its base it is gradually narrowed in a cuneate manner. Typically each pinna has its broadest dimension nearer to its apex than its insertion. There are no auricles at the bases of the forwardly directed margins of the pinnae, and the adaxial face of the rachis is thus not hidden. Numerous slender veins, bifurcating a few times, run fan-wise from the insertion towards the entire margins and apex of a pinna, but the outermost acroscopic veins always run parallel for a short distance with the basal part of the forwardly directed margin and are not foreshortened as those in the basiscopic position.

The cuticle of *Sphenozamites geylerianus* is very fragmentary and it has only been possible to make out certain details of the epidermal pattern. However, there is no doubt that this is the frond of a plant belonging to the Bennettitales. The epidermal cells are rectangular in shape with thin anticlinal walls that are distorted into rounded loops of irregular length. On their outer surfaces one or two cells show an indistinct circular mark which may possibly represent a raised papilla or perhaps a trichome-base. Details of the distribution of the stomata are not known, but several stomata have been observed and it has been possible to make drawings of two of them (Tex-fig. 10 D and E).

The stomatal apparatus is typically bennettitalean in structure (i. e. syndetocheilic) with the guard cells bordered laterally by two elongated subsidiary cells. The guard cells are situated at the bottom of a shallow depression formed by the subsidiary cells which are without papillae on their exposed surfaces. The guard cells are thus completely exposed within the stomatal chamber which has an irregular outline; the width of the opening of the chamber measures the same as the length of the guard cells so that there is no overarching by the polar epidermal cells. The upper and lower walls of the guard cells are cutinised, and the thickening of the upper wall is irregularly plano-convex in surface view with the polar part often prolonged as a sharp projection.

Discussion and Comparison: *Sphenozamites geylerianus* is at once distinguished from *Sphenozamites rossii* by the entire margins of all of its pinnae and the complete lack of any denticulation and spines. An important difference is the general shape of the pinnae which mostly show the broadest dimension nearer to the apex than the insertion. This is not the case with *S. rossii* where the pinnae, particularly those of the mid-region and terminal part of a frond, always show the broadest expansion nearer to the insertion. It should also be noted that the basal pinnae of *S. geylerianus* are elongated and not rounded in form as those of *S. rossii*. A final distinguishing character of external morphology is that the apices of the pinnae of *S. geylerianus* are obtuse, whereas those of *S. rossii* are always acute.

In cuticle-pattern there also differences sufficiently distinct to distinguish the two species. In general, the dimensions of the cells and stomatal apparatus of *S. geylerianus*

are rather less than those of *S. rossii*, but the most marked difference is in the form of the actual stomatal apparatus itself. None of the stomata of *S. geylerianus* show the very large papillae which are so characteristic of the subsidiary cells of *S. rossii*, and the opening of the stomatal chamber of *S. geylerianus* is very different from that of *S. rossii* where it is the shape of an hour-glass.

Seward remarks that the « pinnules » of the Lower Permian *Sphenozamites rochei* Renault are similar in shape to those of *S. geylerianus* [74]. This is not quite true for the pinnae of *S. geylerianus* do not narrow so abruptly towards their bases as do those of the French species from Autun. It should also be remembered that in Renault's original diagnosis of *S. rochei* the pinnae are described as « légèrement décurrentes » [Renault, 60], and that Seward also points out this fact. An examination of both the drawings (Text-fig. 10 A and B) and photographs of the Type-specimen (Plate III, figs. 2 and 3) reproduced here will show that the pinnae of *S. geylerianus* are never decurrent.

RIASSUNTO

La presente memoria costituisce la continuazione delle mie ricerche sulla classica collezione di piante fossili dei calcari grigi del Veneto del Barone Achille De Zigno. Essa contiene nuove descrizioni ed illustrazioni di alcune delle piante che furono descritte e figurate dal De Zigno nel secondo volume della sua magistrale opera intitolata *Flora fossilis formationis oolithicae* (1873-85).

Nella mia prima pubblicazione (uscita nel 1956) sulle piante fossili dei calcari grigi le conifere erano divise, per semplicità, in quattro forme: forme a foglie crasse, disposte a spirale, la cui nervatura non è conosciuta (Forme-generi *Brachyphyllum* Brongn., *Pagiophyllum* Heer e *Dactylethrophyllum* Wesley), forme con foglie ad una sola nervatura (Forma-genere *Elatocladus* Halle *sensu lato*), e forme con foglie a parecchie nervature (Forma-genere *Podozamites* Braun *sensu lato*). Furono allora descritti i primi quattro generi ed io annunciai che, dopo un ulteriore periodo di studio, le forme con foglie a parecchie nervature sarebbero state descritte ed illustrate nella seconda parte delle mie ricerche.

Le descrizioni di queste forme sono ora riportate nella presente memoria, però io non sono convinto che si debba usare per esse il nome *Podozamites*. Nel secondo volume della *Flora fossilis*.... il De Zigno descrisse ed illustrò certi esemplari che assegnò a questa forma-genere (*Podozamites zeillerianus*, *P. plicatus*, *P. hacketi* e *P. rigidus*). Egli non era del tutto sicuro delle sue determinazioni, ma considerò il *Podozamites* come il genere più adatto al quale si potessero attribuire gli esemplari. Tutti gli esemplari, che egli denominò *Podozamites*, sono strutture isolate, allungate, simili a foglie con nervature parallele (infatti, alcuni degli esemplari più piccoli, per quel che si può vedere, sembrano aver avuto una sola nervatura), e non esiste alcun elemento per stabilire se rappre-

sentino foglioline (*pinnae*) staccate di una foglia pennata o se siano, in realtà, delle foglie intere esse stesse. Il nome *Podozamites*, che dapprima voleva indicare le foglie pennate del tipo cicadaleano (Braun), venne poi esteso dallo Schenk in modo da abbracciare anche un asse che porta un numero di foglie semplici parallelinervie, con piccole squame alla base. Il nome viene attualmente inteso in questo senso e non c'è dubbio che alcune delle specie, forse la maggior parte, rappresentino delle conifere, ma è altrettanto probabile che altre (quelle che comprendono foglie veramente pennate) siano delle cicadofite.

Un altro genere simile, ma ad affinità con le ginkgoali, è la *Phoenicopsis*, che è caratterizzata da foglie lineari riunite in fascetti sopra rami brevissimi coperti di squame alla base. In ambedue i generi alcune delle nervature parallele si dividono dicotomicamente almeno una volta vicino alla base della lamina. Spesso si possono attribuire foglie isolate all'uno o all'altro genere quando si accompagnino con esemplari più o meno completi, ma in molti casi non esiste alcun elemento che permetta di stabilire il loro modo di attacco. Per tali esemplari è preferibile il nome meno impegnativo di *Desmiophyllum*. Sfortunatamente questo nome non è entrato nell'uso comune ed esistono molte segnalazioni della presenza di *Podozamites* e *Phoenicopsis* che non sono convalidate da dati adeguati sul modo di attacco. Molte di queste determinazioni sono state fatte perchè i caratteri distintivi che gli autori originali dei generi avevano in mente non sono stati adottati.

Poichè non fu possibile ricavare preparati di cuticola da nessuno degli esemplari italiani e poichè essi non mostrano traccia che le nervature si dividano dicotomicamente vicino alla base, io sono giunto alla conclusione che i dati sono insufficienti per conservare il nome *Podozamites* ed ho pertanto deciso di trasferirli alla forma-genere *Desmiophyllum* (forme con foglie a parecchie nervature). Ho trasferito alla forma-genere *Pityophyllum* i pochi esemplari che, a quanto sembra, hanno posseduto una sola nervatura. Di solito si pensa che il *Pityophyllum* fosse una foglia di conifera, ma ciò non trova alcuna conferma negli esemplari italiani. Credo quindi che gli esemplari denominati *Podozamites* spp. dal De Zigno e che io adesso ridesigno *Desmiophyllum* spp. e *Pityophyllum* sp., possano essere classificati solo come piante di posizione incerta, probabilmente gimnosperme. In conseguenza, gli esemplari del De Zigno sono ridescritti e ri-illustrati come segue: *Desmiophyllum zeillerianum* (già *Podozamites zeillerianus*), *Desmiophyllum rigidum* (già *Podozamites rigidus* e comprendendo gli esemplari italiani attribuiti a *Podozamites plicatus*), *Pityophyllum crassicostatum* (già gli esemplari italiani descritti dal De Zigno come *Podozamites hacketi*). Ciò significa che i *Podozamites* non esistono nella flora liassica italiana e che il numero di generi indiscutibili di conifere si è stabilito in quattro — *Brachyphyllum*, *Pagiophyllum*, *Dactylethrophyllum* e *Elatocladus* — o forse cinque se si include anche il *Pityophyllum*.

La maggior parte del secondo volume della *Flora fossilis....* è dedicata alle descrizioni ed alle illustrazioni delle specie che il De Zigno considerava come rappresentanti delle cicadacee. Gli esemplari sono perloppiù di fronde e alcuni di essi sono molto belli, ma esistono anche parecchi organi riproduttori. Quando il De Zigno scrisse la *Flora fossilis....*, i soli membri delle cicadofite allora conosciute erano le cicadali viventi e naturalmente egli e altri autori contemporanei collocavano le fronde cicadiformi mesozoiche con le cicadali. Dovevano passare degli anni prima che venisse dimostrato che, durante l'era mesozoica, le cicadofite erano rappresentate anche da un altro gruppo che non

conta più membri viventi. Questo gruppo estinto, chiamato le bennettitali, include piante che portavano fronde assomiglianti, nella morfologia esterna, a quelle di molte specie delle cicadali. Oltre alla diversa costruzione dei loro organi riproduttori, le bennettitali differiscono notevolmente dalle cicadali nella struttura distintiva del loro apparato stomatico che è del tipo detto « syndetocheilic ». Così è successo che, in conseguenza dello studio minuzioso delle loro cuticole, molte specie, che già erano attribuite alle cicadali fossili, sono state ora riferite alle bennettitali.

La raccolta del De Zigno contiene molti begli esemplari che conservano ancora traccie del materiale originario delle piante sulla superficie della roccia, e sono sicuro che, quando avrò terminato le mie ricerche microscopiche sulle loro cuticole, bisognerà trasferire la maggioranza delle specie alle bennettitali. E' già stato necessario fare così per i campioni italiani dello *Sphenozamites* e in conseguenza delle mie estese indagini su tutti gli esemplari ho cercato di stabilire la validità della forma-genere *Sphenozamites*, però entro limiti più ristretti di quanto non si intendesse finora.

Il nome *Sphenozamites* fu proposto nel 1849 dal Brongniart come un sotto-genere di fronde cicadiformi che erano state in precedenza assegnate alla forma-genere *Otozamites*. Il nuovo nome doveva indicare foglie pennate sulle quali le foglioline, con le caratteristiche nervature dicotome in modo flabellato, si attenuavano verso le loro basi in forma di cuneo e mancavano di un'orecchietta basilare ben pronunciata come nel vero *Otozamites*. Il Brongniart cita « *Cyclopteris Beani* » come illustrativo del nuovo sottogenere, ma non si può comprendere il perchè: questa fronda fossile è caratterizzata dalle foglioline che mostrano i loro margini basilari anteriori allargati come orecchiette arrotondate che ricoprono la faccia adassiale del rachide come avviene nelle vere specie del genere *Otozamites*. Per questi motivi, seguendo altri autori, il De Zigno la manteneva giustamente in questo genere (cioè il genere *Otozamites*). Il Brongniart propose che si elevasse eventualmente lo *Sphenozamites* al grado generico e questo fu fatto, però in senso troppo ampio, dal De Zigno nel secondo volume della *Flora fossilis formationis oolithicae*. L'identità generica dello *Sphenozamites* fu riconosciuta da numerosi autori che lo conservarono come nome pratico per descrivere forme non facilmente attribuibili ad altri generi, ma è da notare che alcuni di questi autori hanno usato il nome in un senso più restrittivo degli altri.

La posizione dello *Sphenozamites* nel sistema naturale di classificazione rimaneva sconosciuta fino a che il Linell non riesaminò la specie keuperiana *Sphenozamites tener*, però in generale si aveva l'abitudine di considerare il genere come inclusivo delle fronde di piante appartenenti alle cicadofite (cioè ad affinità cicadaleana o bennettitaleana) piuttosto che alle pteridofite. Le ricerche del Linell sulla cuticola di *Sphenozamites tener* provarono le affinità cicadofite di quella specie, ed i caratteri generali dell'epidermide e la costruzione dell'apparato stomatico lo indussero ad assegnare la specie ad una posizione vicina alle nilssoniali.

Mancavano del tutto informazioni sulle altre specie dello *Sphenozamites*, ma le mie ricerche più recenti sulla struttura delle specie italiane, assegnate dal De Zigno a questo genere e accettate dal Linell come specie valide dello *Sphenozamites* per ragioni morfologiche, mi hanno messo in grado di dimostrare in modo sicuro che esse sono delle vere rappresentanti delle bennettitali.

I caratteri principali delle cuticole delle due specie italiane, *Sphenozamites rossii* e *S. geylerianus*, delle quali sono date ampie descrizioni ed illustrazioni, si conformano esattamente a quei caratteri pei quali si distinguono le fronde delle bennettitali da quelle di altre gimnosperme fossili a foglie pennate. La cuticola delle bennettitali è caratterizzata dalla struttura ben distinta dell'apparato stomatico e dagli strati cutinizzati delle cellule di chiusura. L'apparato stomatico è del tipo detto « syndetocheilic » che, a parte i generi viventi *Welwitschia* e *Gnetum*, si presenta solamente nelle bennettitali estinte. Questo tipo di apparato stomatico consiste di due cellule di chiusura fiancheggiate lateralmente da due cellule accessorie, le quattro cellule essendo derivate da divisioni parallele di una sola cellula-madre iniziale. Per giunta, le pareti dorsali e le pareti esterne delle cellule di chiusura (rispettivamente pareti superiori e pareti esterne della mia terminologia) sono spiccatamente cutinizzate e spesso la cutinizzazione della parete dorsale (superiore) si è sviluppata di più nella regione dove essa si estende nella parete comune fra la cellula di chiusura e la sua contigua cellula accessoria. Caratteri meno costanti del gruppo sono l'orientazione trasversa delle fenditure degli stomi e l'ordinamento delle cellule epidermiche in file longitudinali ben distinte e di solito a pareti anticlinali ondulate.

Così il genere *Sphenozamites*, come venne definito per il passato, non rappresenta più al giorno d'oggi un raggruppamento naturale di specie ed è chiaro che il nome non può essere applicato validamente a tutte le forme già descritte. Diventa quindi necessario ridesignare subito la forma-genere *sensu stricto* in modo da includere soltanto un unico gruppo di specie. Con quali caratteri, perciò, si potranno distinguere le specie ad apparati stomatici delle bennettitali (a) dalle forme caratterizzate da una morfologia esterna molto simile ma con apparati stomatici non del tipo delle bennettitali, e (b) dalle forme strettamente collegate che appartengono alle bennettitali?

Le uniche specie delle quali si conosce la struttura della cuticola sono *Sphenozamites tener* (apparato stomatico del tipo detto « haplocheilic », cioè le cellule di chiusura e le cellule accessorie avendo origine da cellule-madri diverse durante il loro sviluppo, e le cellule epidermiche disposte in modo irregolare e a pareti anticlinali non ondulate) e *S. rossii* e *S. geylerianus* (apparato stomatico del tipo « syndetocheilic », cioè le cellule di chiusura e le cellule accessorie derivate dalla stessa cellula-madre iniziale durante il loro sviluppo, e le cellule epidermiche ordinate in file longitudinali e a pareti anticlinali ondulate). Poichè le due specie italiane si differenziano talmente nella struttura della cuticola bisogna cercare altri caratteri a mezzo dei quali sia possibile distinguerle da *Sphenozamites tener*. Il Linell pubblicò una diagnosi emendata del genere che include i caratteri tipici tanto di *Sphenozamites tener* quanto di tutte le altre specie assegnategli. Quindi si può interpretare la parte morfologica della sua diagnosi fra limiti ampii. Le due specie italiane si accordano soltanto in riguardo di certi caratteri, ma differiscono sotto altri aspetti. *Sphenozamites rossii* e *S. geylerianus* si accordano per quanto segue: la fronda è costruita apertamente; le foglioline sono alterne, più o meno spiegantisi e di forma più o meno asimmetrica; le basi delle foglioline si attenuano in forma di cuneo, non ricoprono mai una parte del rachide e non sono mai auricolate; le nervature dicotome in modo flabellato. Non mostrano i caratteri seguenti che sono quelli più tipici di *Sphenozamites tener* stesso: la foglia con le foglioline disposte in due serie opposte e con una fogliolina terminale impari; le foglioline opposte e attaccate piuttosto sulla faccia

adassiale del rachide; il margine basiscopico della fogliolina più lungo del margine acroscopico; la base della fogliolina ristrettasi in un breve picciuolo.

E' logico, perciò, che queste due serie di caratteri rappresentino i più importanti criteri morfologici in base ai quali sia possibile distinguere le specie italiane da *Sphenozamites tener*. Questa separazione ha reso necessaria l'istituzione di una nuova forma-genere oltre allo stesso *Sphenozamites*, perchè non si può più usare tale nome per fronde caratterizzate da una struttura così diversa della cuticola. *Sphenozamites rossii* fu descritto ed illustrato dal De Zigno nel 1868, mentre il Compter adoperò il nome *Sphenozamites tener* per la prima volta nel 1883. Aderendo alle regole della priorità si deve mantenere la designazione generica per le specie italiane e per tutte le altre fronde simili che eventualmente mostrassero di aver la cuticola a struttura delle bennettitali. Così *Sphenozamites tener* non è più una combinazione valida e ho creato un nuovo nome per la specie — quello di *Apoldia tenera* — e l'ho designato il generitipo della nuova forma-genere *Apoldia*, della quale ho dato una diagnosi più ristretta.

Benchè io abbia dimostrato chiaramente le affinità delle specie italiane, non mi è stato possibile stabilire alcun carattere particolare della struttura della cuticola che si potesse usare per definire lo *Sphenozamites* come un genere naturale, perchè non c'è neppure alcuna caratteristica della cuticola che possa separarlo dalle altre forme-generi delle bennettitali.

Cinque forme-generi appartenenti alle bennettitali a foglie del tipo pennato sono di solito riconosciute e vengono definite dalla forma delle basi delle foglioline. Si può disporre questi caratteri in forma di tabelle come segue:

	angolo basilare anteriore	angolo basilare posteriore
Ptilophyllum	ristretto	decorrente
Zamites	ristretto	ristretto (simmetricamente)
Otozamites	allargato e poi ristretto (cioè auricolato)	ristretto (asimmetricamente)
Pterophyllum	non ristretto	non ristretto
Anomozamites	non ristretto	non ristretto

L'*Anomozamites* e il *Pterophyllum* si assomigliano, ma l'*Anomozamites* ha le foglioline più corte. Un altro carattere relativamente costante di queste forme-generi, che si potrebbe aggiungere a questa tabella, è quello della posizione dell'inserzione delle foglioline sul rachide. Nei generi *Ptilophyllum*, *Zamites* e *Otozamites* le foglioline sono attaccate sulla faccia adassiale del rachide, invece nelle forme-generi *Pterophyllum* e *Anomozamites* i segmenti della foglia sono inseriti più o meno lateralmente sul rachide e non ricoprono mai la sua faccia adassiale.

Credo che la forma-genere *Sphenozamites*, la quale secondo la mia proposta andrebbe più circoscritta di quanto non lo fosse in precedenza, non possa essere convenientemente sistemata con alcuna delle cinque forme-generi predette. L'inserzione laterale delle sue foglioline distingue immediatamente le fronde da quelle attribuite alle forme-generi *Ptilophyllum*, *Zamites* e *Otozamites*, le quali presentano tutte le foglioline inserite sulla faccia adassiale del rachide. Non rimangono disponibili che i generi *Pterophyllum* e *Anomozamites*. Però queste due ultime forme-generi sono caratterizzate da foglioline che non presentano l'uno o l'altro angolo basilare ristretto. Questo non è il caso dello *Sphenozamites*, in cui le foglioline si riducono gradualmente verso le loro basi a guisa di cuneo.

Le basi cuneiformi delle foglioline furono sempre considerate come il più importante carattere generico della forma-genere *Sphenozamites*, ma la mancanza di un'orecchietta sul margine anteriore di ogni fogliolina, che avrebbe dovuto ricoprire il rachide, non è stata mai pubblicata nelle varie diagnosi della forma-genere. Sembra che questo carattere abbia rappresentato l'ostacolo maggiore per distinguere lo *Sphenozamites* dallo *Otozamites*, perchè molte forme dell'*Otozamites* a foglioline strette spesso non presentano l'auricola ben marcata. Per quanto riguarda la forma delle loro foglioline non c'è alcun dubbio che lo *Sphenozamites* e alcune specie dell'*Otozamites* si rassomigliano strettamente.

Non credo però che la nervatura delle foglioline dello *Sphenozamites*, come ora definito più strettamente nella mia diagnosi emendata, offra un qualsiasi indizio di un'auricola sul margine anteriore. Tutti gli esemplari che io ho esaminato mostrano molto chiaramente che i nervetti acroscopici più esterni sono paralleli per una breve distanza alla parte basilare del margine anteriore di una fogliolina, e non c'è alcuna indicazione in qualsiasi luogo che la loro direzione cambi o che essi terminino ove dovrebbe svilupparsi un'orecchietta. Questa differenza fra lo *Sphenozamites* e l'*Otozamites* io la ritengo molto importante.

Furono inoltre passate in rassegna tutte le altre specie attribuite alla forma-genere *Sphenozamites*, constatando che alcune delle determinazioni non erano state eseguite con la dovuta accuratezza. In ogni modo, fino a quando non si avranno maggiori conoscenze sulla struttura della cuticola di queste specie, ogni loro nuova sistemazione non potrà avvenire che per tentativi. Si dovrà poi usare molta cautela nell'attribuire il nome *Sphenozamites* a esemplari provenienti da parecchi orizzonti stratigrafici ben separati nella scala verticale del tempo. Io ritengo per certo che non sia giustificato l'uso del nome *Sphenozamites* per le fronde fossili trovate nei terreni che vanno dal Permo-Carbonifero al Giurassico, ma poichè le nostre conoscenze sono così scarse, un aumento del numero dei nomi generici non condurrebbe che alla confusione.

Il De Zigno descrisse quattro specie provenienti dai calcari grigi del Veneto — *Sphenozamites rossii*, *S. lanceolatus*, *S. adiantifolius* e *S. geylerianus* — ma in seguito alle mie ricerche esse sono state ridotte a due (*S. rossii* e *S. geylerianus*). Un esame microscopico delle cuticole di *S. rossii*, *S. adiantifolius* e *S. lanceolatus* mi ha persuaso che tutte tre rappresentino una sola specie, *Sphenozamites rossii*. Certamente le denticolazioni dei margini delle foglioline sono variabili, ma ogni esemplare è caratterizzato da foglioline basali a margini spinosi ben sviluppati e da foglioline terminali a margini interi.

Non si osservano che alcune variazioni nella parte mediana delle fronde, dove la forma delle foglioline è anche piuttosto variabile. Non ritengo che queste variazioni di morfologia esterna assumano importanza specifica (variazioni analoghe si presentano abitualmente nelle fronde pennate di piante viventi) e ripongo maggiore fiducia nella straordinaria costanza delle caratteristiche della cuticola.

Venne compiuta un'accurata comparazione di *Sphenozamites rossii* e *Otozamites beani*, perchè certi autori hanno voluto considerarle come una sola specie. Questi autori osservavano che le foglioline di *Sphenozamites rossii* non erano spinose e che i margini irregolarmente dentellati erano il risultato del laceramento di una lamina intera. Credo che non si possano mai confondere le due specie, perchè le fotografie di *Sphenozamites rossii* mostrano senza dubbio che i margini delle foglioline basilari presentano sempre denticolazioni spiniformi e non sono intere come quelle di *Otozamites beani*. Un carattere così costante nella stessa posizione in un gran numero di esemplari non si può spiegare come il risultato della probabilità. Infine una prova decisiva e convincente della indipendenza delle due specie si ricava dallo studio comparativo dei loro apparati stomatici. La cavità stomatica poco profonda di *Sphenozamites rossii*, caratterizzata dal suo orifizio a foggia di clessidra e dalle grandi papille sulle cellule accessorie, non assomiglia per nulla alla cavità profonda di *Otozamites beani* che si apre alla superficie dell'epidermide con un orifizio molto costretto e lobato.

L'altra specie italiana, *Sphenozamites geylerianus*, è chiaramente diversa da *S. rossii*. Si distingue tanto per la forma piuttosto diversa delle foglioline quanto per i margini sempre interi. Esistono anche alcune differenze nella struttura della cuticola, la più importante delle quali è la forma dell'apparato stomatico. Nessuno degli stomi di *Sphenozamites geylerianus* mostra le grandissime papille che sono così caratteristiche per le cellule accessorie di *S. rossii*, e l'orifizio della cavità stomatica è molto diverso non avendo la foggia di una clessidra.

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PLATE I.

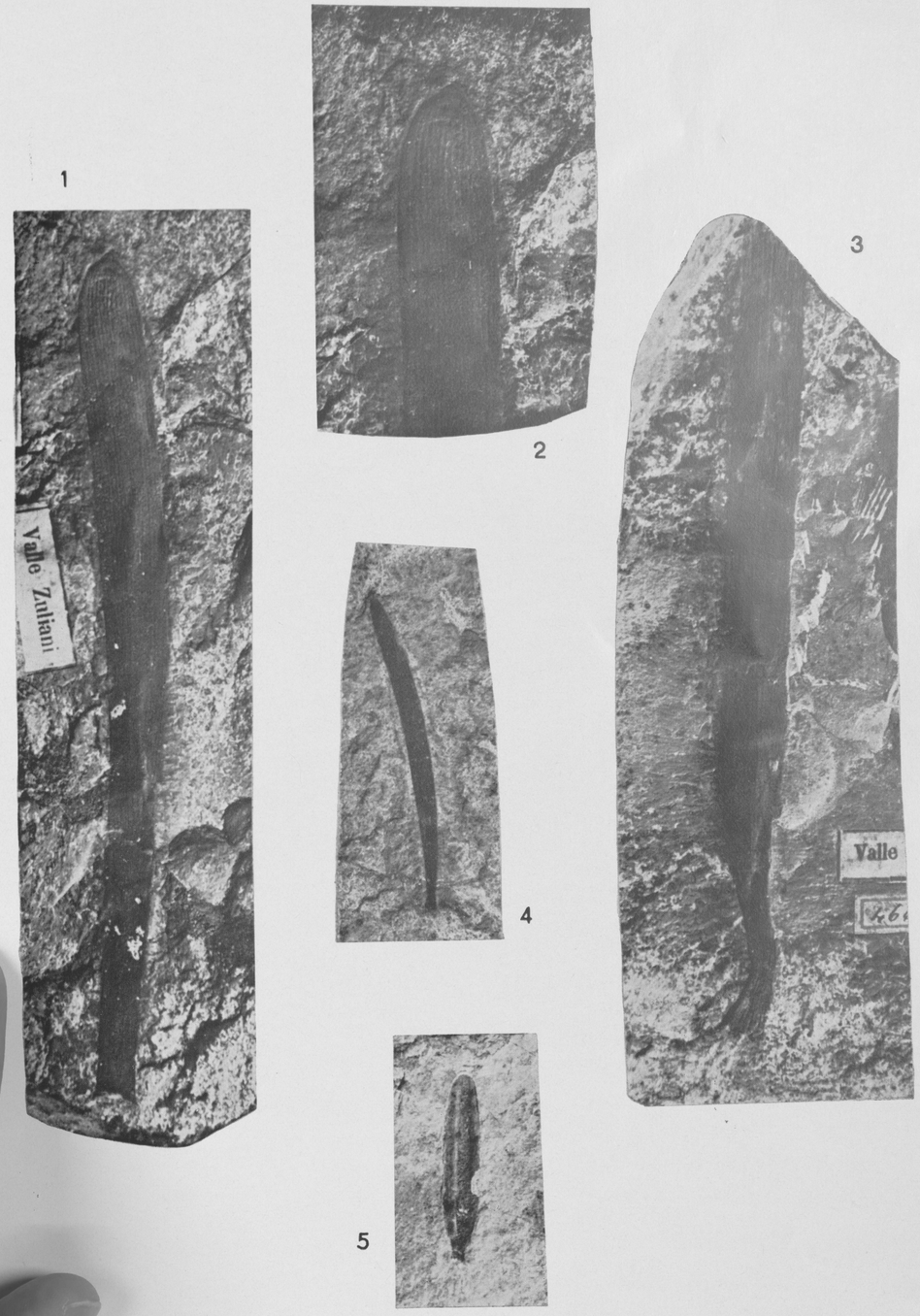
EXPLANATION OF PLATE I.

Figs. 1 - 3. *Desmiophyllum zeillerianum* (Zic.) n.comb.

1. Specimen No. 4665; syntype of *Podozamites zeillerianus* Zic.; complete specimen. Valle Zulliani. Natural size.
2. Apical part of same specimen enlarged to show the endings of the veins. X 1.5.
3. Specimen No. 4667; syntype of *Podozamites zeillerianus* Zic.; complete specimen. Valle Zulliani. Natural size.

Fig. 4. *Desmiophyllum rigidum* (Zic.) n.comb. - Specimen No. 4649; syntype of *Podozamites rigidus* Zic. Valle Zulliani. Natural size.

Fig. 5. *Pityophyllum crassicostatum* sp.nov. - Type-specimen No. 4659. Pernigotti. X 1.5.


1
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4
5
Valle Zulliani
Valle

PLATE II.

EXPLANATION OF PLATE II.

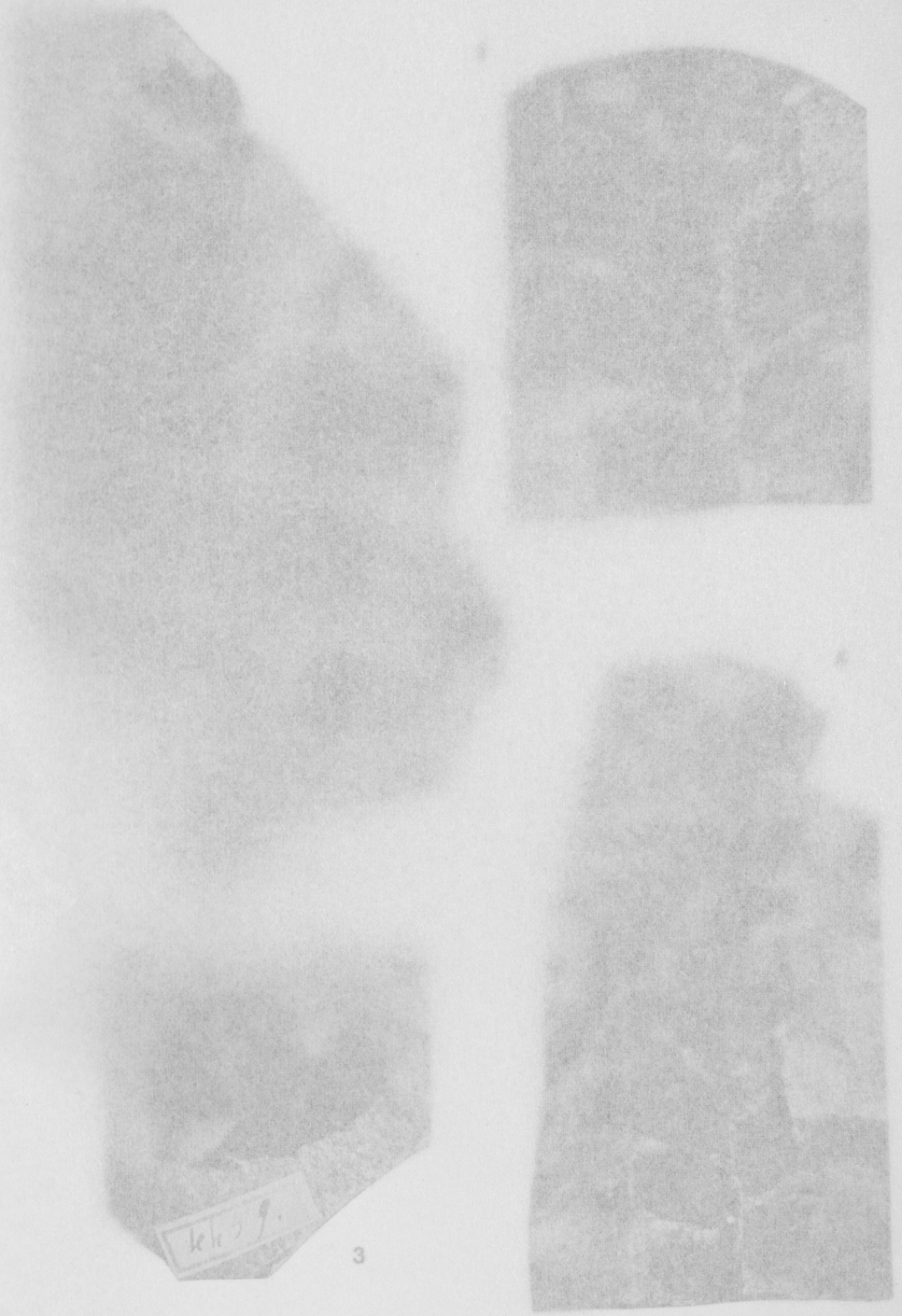
Figs. 1 - 4. *Sphenozamites rossii* Zig.

1. Type-specimen proper No. 4453; the terminal part of the frond, represented by the three pinnae on specimen No. 4400 (Text-fig. 4 A), is not shown here. Rotzo. Natural size.

2. Specimen No. 4441; syntype of *Sphenozamites adiantifolius* Zig.; lower part of specimen. Rotzo. X 1.5.

3. Specimen No. 4459. Rotzo. X 1.5.

4. Specimen No. 4441; syntype of *Sphenozamites adiantifolius* Zig.; complete specimen. Rotzo. Natural size.



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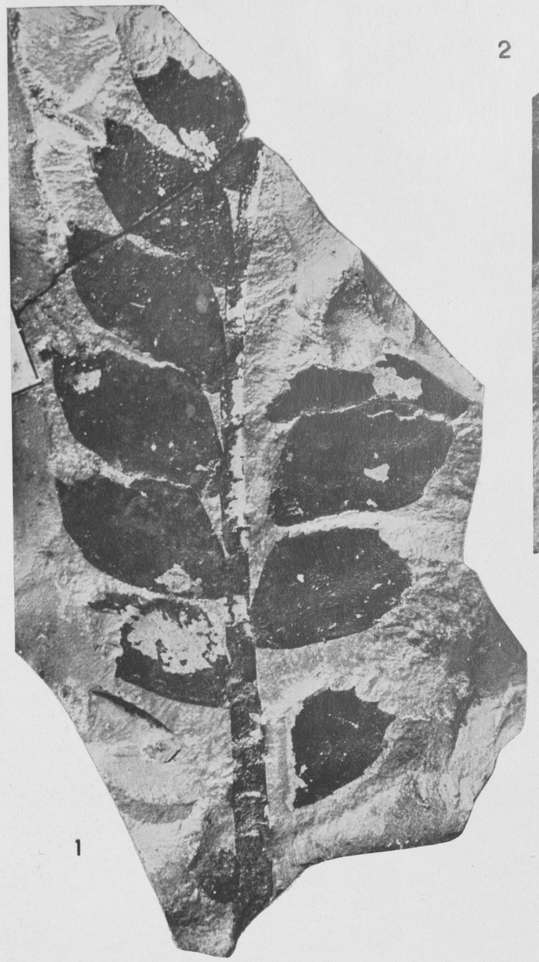

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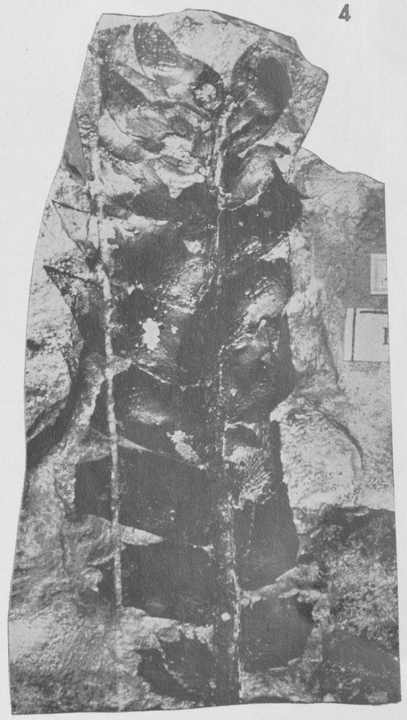

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PLATE III.

EXPLANATION OF PLATE III.

Fig. 1. *Sphenozamites rossii* Zic. - Upper part is specimen No. 4412, lower part is specimen No. 4458; the complete frond is a syntype of *Sphenozamites lanceolatus* Zic. Rotzo. Natural size.

Figs. 2 - 3. *Sphenozamites geylerianus* Zic.

2. Type-specimen No. 4399; central part of specimen enlarged to show venation. Valle Zulliani, near Roverè di Velo. X 2.

3. Type-specimen No. 4399; complete specimen. Natural size.

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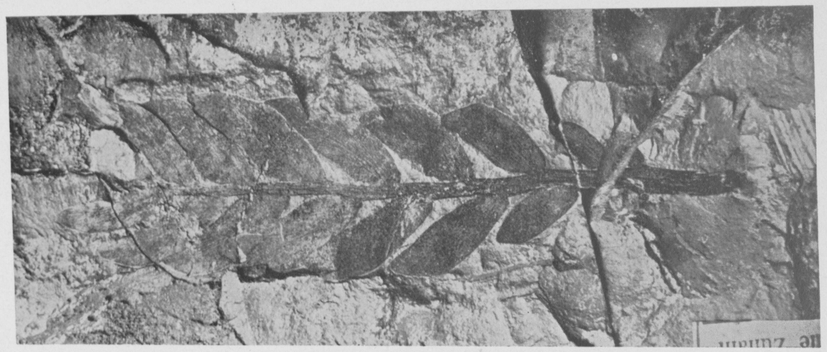

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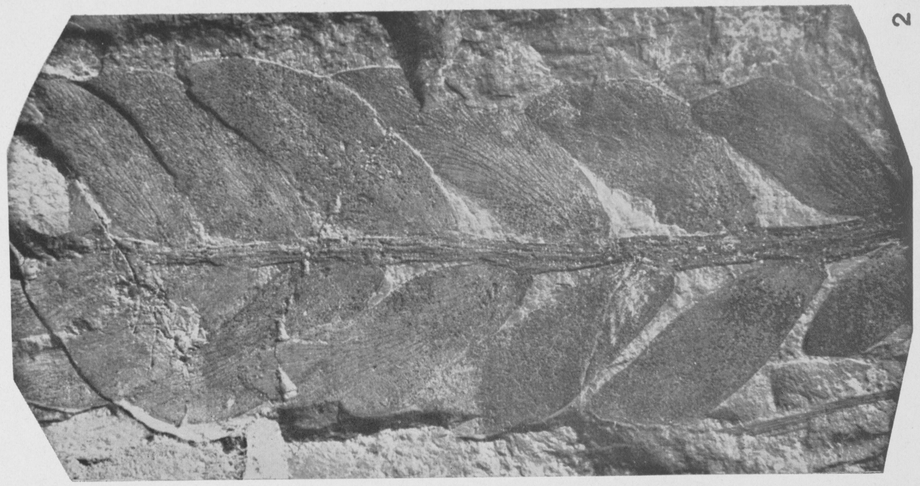

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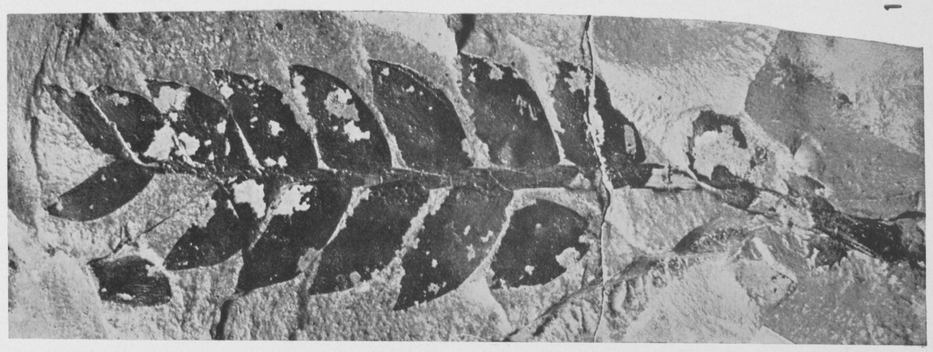

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